A.J. Gaston
(with foreword by W.A. Montevecchi)

Studies of high-latitude seabirds. 5. Monitoring Thick-billed Murres in the eastern Canadian Arctic, 1976–2000

Occasional Paper
Number 106
Canadian Wildlife Service

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102-06925/

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[1] Canadian Wildlife Service, National Wildlife Research Centre, Hull, Quebec K1A 0H3.

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Cover photo: Thick-billed Murres at Coats Island in high winds. (T.J.F. Lash)

Published by Authority of the
Minister of the Environment
Canadian Wildlife Service

© Minister of Public Works and Government Services Canada, 2002
Catalogue No. CW69-1/106E
ISBN 0-662-32174-X
ISSN 0576-6370

National Library of Canada cataloguing in publication data

Gaston, A.J.

Studies of high-latitude seabirds. 5. Monitoring Thick-billed Murres in the eastern Canadian Arctic, 1976–2000

(Occasional paper, ISSN 0576-6370; no. 106)
Includes an abstract in French.
Includes bibliographical references.
ISBN 0-662-32174-X
Cat. no. CW69-1/106E

1. Seabird — Arctic Coast (Canada).
2. Water birds — Arctic Coast (Canada).
3. Thick-billed murre — Arctic Coast (Canada) — Geographical distribution.
I. Gaston, A.J.
II. Montevecchi, William A.
III. Canadian Wildlife Service.
IV. Series: Occasional paper (Canadian Wildlife Service); no. 106.

QL671.G37.2002 598.2971 C2002-980137-0

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Foreword

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It is widely accepted that wisdom is nurtured by experience and age. Yet as our knowledge increases, so does our appreciation of the uncertainties in which that knowledge is embedded. This is especially evident in our growing understanding of the environment and of the nonhuman creatures that share it with us. In this respect, environmental wisdom is tempered with an appreciation of the interplay between our knowledge and our ignorance. The more we learn, the less simple and the less certain the answers become.

Through immersion in long-term studies of Thick-billed Murres in the Canadian Arctic as the major part of his life's work, Tony Gaston has learned these lessons well. The investigations published here exemplify the type of research that is needed to improve our understanding of marine ecosystems and of their truly incredible inhabitants. As Leslie Tuck (1961) foretold a couple of decades before Tony began his Arctic studies with David Nettleship (Gaston and Nettleship 1981), Thick-billed Murres are vital manifestations of the Arctic ecosystems in which they live, mate, rear offspring, and die, as generational waves wash over one another through the evolutionary tides of environmental change.

The hunt of Thick-billed Murres in Newfoundland and Labrador is considered to represent a major source of adult mortality. The first contribution in this publication details an investigation to assess whether seasonal and bag limits imposed in 1993 to reduce winter hunt harvests in Newfoundland by 50% had measurable effects on the breeding population of Thick-billed Murres on Coats Island, Nunavut. No effect was detected in the survival of breeding adults, which remained relatively steady at about 90% per annum. Band recoveries by hunters of first-winter birds in Newfoundland exhibited no significant trends through the 1980s and 1990s, whereas band recoveries from murres 2 years of age and older, especially breeding-age birds, declined sharply after 1990. These findings suggested that breeding-age Thick-billed Murres changed their wintering distributions in Newfoundland waters, making them less vulnerable to hunters. This timing interestingly coincided with a major regime shift (Steele 1998) in the Northwest Atlantic. During the 1990s, primary forage and pelagic fishes exhibited significant distributional changes, some of the initial indications of which came from studies of the feeding ecology of seabirds that breed in Newfoundland (Montevecchi and Myers 1992, 1996) and Labrador (Bryant et al. 1999). Thick-billed Murres, it appears, integrate a dynamic interplay among High and Low Arctic ecosystems and the interactive influences of human hunters.

The second contribution in this publication reports on the results of 25 years of effort in monitoring populations of Thick-billed Murres in the eastern Canadian Arctic. The number of colonies consistently monitored is not as extensive as one (including Tony Gaston) might hope. However, very considerable effort has been involved, and Gaston compiles all of the systematic information that is available. These archival data and especially the photographic information provided in Appendix 1 will undoubtedly be invaluable to researchers in the future who, like Tuck and Gaston before them, will revisit questions of long-term population dynamics and environmental change. Murre populations at Coats and Prince Leopold islands appear to have decreased between 1989 and 1991, whereas those at Digges Island likely declined between 1985 and 1990. All colonies appear relatively stable at present, and the counts go on. Consistent population trends among distant Arctic colonies again suggest that circumstances on wintering grounds in the Low Arctic waters of the Labrador Sea have major influences on breeding populations in the High Arctic. Clearly, to understand the population dynamics of Thick-billed Murres, it is essential to unravel the environmental influences occurring in their habitats in High and Low Arctic ocean regimes.

From a professional perspective, it is encouraging to see this research continuing. It is also encouraging to see it published in the Canadian Wildlife Service Occasional Papers as the fifth contribution of the "Studies of high-latitude seabirds" series that Tony and I initiated at an international seabird workshop at Memorial University of Newfoundland in 1989 (Montevecchi and Gaston 1991). From both a professional and a personal view, it's good to see Tony Gaston doing what he does best.

Finally, I thank Rob Barrett, David Cairns, Kees Camphuysen, and Scott Hatch for comprehensive and insightful reviews of these contributions, which greatly benefited Tony and me.

Have changes in hunting pressure affected the Thick-billed Murre population at Coats Island, Nunavut?

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Abstract

Hunting of Thick-billed Murres *Uria lomvia* in winter off Newfoundland and Labrador is thought to be a major cause of adult mortality for the populations involved. Regulations for this hunt were adjusted in 1993 to effect a 50% reduction in the harvest. I examined trends in banding recoveries and population parameters for the breeding colony at Coats Island in northern Hudson Bay to see whether the intended reduction in the harvest level had measurable effects on the population.

Banding recoveries of first-winter birds showed no change over the period considered (bandings in 1984–1998, recoveries up to 2000–2001 winter), but recoveries of birds more than 2 years old, especially breeding-age birds, decreased sharply around 1990. The difference in trends between age classes suggested that a change in the wintering behaviour of birds in their third year and older took place about 1990, making them less likely to be killed by hunters. There was no indication that the change in regulations affected the survival of breeding adults, which remained fairly constant at about 90% per annum. This observation was consistent with the virtual disappearance of breeding-age birds from the hunting recoveries after 1990. An improvement in the recruitment of 4- and 5-year-olds was noted after 1996, coinciding with the recruitment of cohorts reared subsequent to the change in regulations. This improved recruitment may have been the result of reduced hunting pressure on birds in their second year.

It appears that environmental changes preceding the changes in hunting regulations may have preempted the intended effect of the new regulations, causing them to have little impact on the Coats Island population.

Résumé

On croit que la chasse hivernale au Guillemot de Brünnich (*Uria lomvia*) au large de Terre-Neuve-et-Labrador est une cause importante de la mortalité chez les adultes dans les populations concernées. On a modifié le règlement de cette chasse en 1993 afin de diminuer les prises de 50 p. 100. J'ai examiné les tendances de la récupération de bagues et les paramètres de population de la colonie de reproduction à l'île Coats, dans le Nord de la baie d'Hudson, afin de déterminer si la réduction souhaitée du nombre de prises avait des incidences mesurables sur la population.

Les bagues récupérées des oiseaux vivant leur premier hiver n'ont indiqué aucun changement au cours de la période étudiée (le baguage de 1984 à 1998; les récupérations jusqu'à l'hiver 2000-2001), mais la récupération de bagues provenant d'oiseaux de plus de deux ans, surtout d'oiseaux en âge de se reproduire, a diminué de manière significative vers 1990. Les différentes tendances entre les groupes d'âge semblent indiquer que les oiseaux de trois ans et plus ont modifié leur comportement d'hivernage vers 1990, ce qui les a rendus moins vulnérables aux chasseurs. Rien ne signale que les changements apportés au règlement ont eu une incidence sur la survie des adultes nicheurs, laquelle se maintient à un taux approximatif de 90 p. 100 par année. Cette observation est conforme à la disparition quasi complète des prises d'oiseaux en âge de se reproduire après 1990. On a remarqué une augmentation du recrutement d'oiseaux de quatre et de cinq ans après 1996, ce qui coïncide avec le recrutement de cohortes élevés après la modification du règlement. Ce recrutement amélioré est peut-être attribuable à la diminution des pressions de chasse sur les oiseaux de deux ans.

Il semble que les changements de l'environnement qui ont précédé les modifications du règlement de chasse auraient pu aller à l'encontre des effets recherchés par les nouveaux règlements, ce qui a fait en sorte qu'ils aient eu peu de répercussions sur la population de l'île Coats.

1. Introduction

Manipulation of hunting regulations is a tool commonly used in the management of hunted populations, but the contributions of changes in hunting regulations to population dynamics are seldom assessed. In 1993, a substantial change was made to regulations governing the legal harvest of Thick-billed Murres *Uria lomvia* in Newfoundland and Labrador. The change was imposed on a situation where hunting was believed to be a major cause of adult mortality (Elliot 1991; Gaston et al. 1994). This paper examines evidence for population consequences resulting from the change in regulations.

Thick-billed Murres from breeding colonies in the eastern Canadian Arctic and West Greenland, along with

smaller numbers of birds from colonies in the eastern Atlantic, winter in large numbers in waters off eastern Canada (Gaston 1980; Kampp 1988). They are hunted in winter by residents of Newfoundland and Labrador, a practice that is centuries old (Tuck 1961). From 1949, when Newfoundland joined Canada, a hunting season of 5 months (November–March) with no bag limits was allowed (Elliot 1991), and no licence was required. During the 1970s, the annual harvest ranged from 600 000 to 900 000 birds (Wendt and Cooch 1984; Elliot et al. 1991) from a wintering population believed to be in the order of 4 million (Gaston 1980). Harvests in the 1980s and early 1990s were considered to be in the order of 500 000 birds (Chardine et al. 1999).

Restrictions on the hunting of murres off Newfoundland and Labrador were introduced on an emergency basis in the winter of 1991–1992 because of reports of very large harvests of murres (true numbers were unknown, but were considered by local hunters to be very high) on the southeast coast of Newfoundland (J. Chardine, pers. commun.). The season was closed on 10 March instead of at the end of the month, and this early closing was repeated in 1992–1993. Since 1993–1994, more comprehensive restrictions, including bag, possession, and season limits, have been enforced every year. The restrictions were introduced because the estimated harvest during the 1980s (Elliot et al. 1991; Chardine et al. 1999) was considered unsustainable in the long term, on the basis of computer models of the population (J. Chardine, pers. commun.). There was no definite evidence that the Canadian population had declined since effective monitoring began in the mid-1970s (Gaston et al. 1993; Gaston 1999). However, the murre population of West Greenland, where substantial numbers were shot during the breeding season for commercial sale, was known to have declined substantially between the 1940s and 1990s (Evans and Kampp 1991; Falk and Durinck 1992; Kampp et al. 1995). Many first-year birds from West Greenland are killed in the Newfoundland hunt (Donaldson et al. 1997). Hence, depleted populations in West Greenland also stood to benefit from reductions in the Newfoundland harvest.

Although the harvest was known to have decreased between the 1970s and 1980s (Chardine et al. 1999), scientists, managers, and hunters all felt that prudence required a significant further reduction in the numbers killed. Restrictions were designed to achieve a 50% reduction in the total number of birds killed, while allowing equal access for different communities. Evidence from harvest surveys suggests that this aim was achieved (Figure 7 in Chardine et al. 1999).

Because Thick-billed Murres reproduce slowly (age at first breeding 4–6 years, maximum annual productivity 1 young/pair; Gaston et al. 1994), it was thought that they were probably more sensitive to hunting mortality than species reproducing more rapidly (Evans and Nettleship 1985). Moreover, estimates of adult survival for Thick-billed Murres breeding in Canada and Greenland suggested that annual adult mortality of these hunted populations was higher, perhaps by as much as 40%, than might be expected on the basis of estimates for eastern Atlantic populations of the congeneric Common Murre *Uria aalge*, which is not hunted (Kampp 1991; Gaston et al. 1994; Kampp et al. 1995). These observations led to the expectation that a substantial reduction in the harvest, especially of breeding-age birds, would have a strong effect on the population trend.

It is not possible to obtain a rigorous estimate of the effect of the hunting restrictions instituted in 1993, because there was no control area available where birds continued to be shot in their former numbers. Most of the Thick-billed Murres that winter in the Northwest Atlantic do so in waters off southern Greenland, in the Labrador Sea, and off Newfoundland. It is probable that most birds breeding in Greenland or the eastern Canadian Arctic are at risk from hunting in Newfoundland at some time in their lives (Kampp 1988, 1991; Donaldson et al. 1997). Seabird populations, including those of murres, are known to fluctuate widely over a scale of decades in response to changes in oceanography and food stocks (Cairns 1992). Murres are also very susceptible to mortality from oil pollution, a common, but unmeasured, occurrence around Newfoundland (Piatt et al. 1985, 1991; Chardine and Pelly 1994; Wiese and Ryan 1999). Hence, changes in Thick-billed Murre populations coincident with, or subsequent to, the institution of hunting restrictions in Newfoundland in 1993 can provide only circumstantial evidence, rather than proof, of the effectiveness of the restrictions.

Thick-billed Murres have been banded at several colonies in the eastern Canadian Arctic periodically since 1955 (Tuck 1961; Gaston 1980). Of these colonies, the most comprehensive data set is available for Coats Island, in northern Hudson Bay, where adults and nestlings have been banded annually since 1984 and numbers monitored annually since 1985. I use these data to assess changes since 1984 in banding recoveries, population trends, numbers of occupied breeding sites, recruitment of first-time breeders, and year-to-year survival of breeding adults for the Thick-billed Murre population breeding at Coats Island. The proportion of Thick-billed Murres banded at Coats Island that have been recovered in Newfoundland is similar to the proportion of those banded at Coburg Island in the High Arctic during the same years and higher than the proportion from Digges Island in western Hudson Strait (Donaldson et al. 1997). Hence, changes in population observable at Coats Island in response to changes in hunting mortality should be as great as those occurring for other Canadian populations. The possible role of the hunting restrictions introduced in 1993 in causing changes in population parameters is discussed.

2. Methods

2.1 Study area

Gaston et al. (1993) described the Thick-billed Murre breeding sites at Coats Island. The murres breed on two cliffs separated by about 1.5 km. All of the banding and observations described here were performed at the western colony, which supports about 18 000 breeding pairs.

2.2 Banding recoveries

Banding of nestlings at Coats Island took place annually from 1984 to 1998, with 1316–2686 banded each year (for methods, see Gaston and Donaldson 1994). The current analysis considers only those birds recovered (i.e., shot and reported) by hunters in Newfoundland and Labrador. More than 90% of all recoveries of Thick-billed Murres banded at colonies in Hudson Strait and northern Hudson Bay came from that province; among these, more

than 95% were shot (Donaldson et al. 1997). About half of all recoveries were of birds in their first winter, and recoveries declined with age (Donaldson et al. 1997). Recoveries of birds banded as nestlings were analyzed as a percentage of those banded each year. Recoveries of birds older than 2 years were sparse, and those recovered at 3–6 years of age were amalgamated for analysis. Previous studies suggest that birds more than 2 years of age behave similarly in winter (Kampp 1982; Donaldson et al. 1997). For comparison with recoveries of cohorts at 3–6 years of age, first-year recoveries for the same 4-year periods were combined (e.g., recoveries of the 1984 cohort at 3–6 years were compared with the sum of recoveries of first-year birds in the 1986–1987, 1987–1988, 1988–1989, and 1989–1990 winters).

Numbers of adults banded annually at Coats Island ranged from 85 to 346. Because recovery rates for this group were very low, recoveries of birds banded as adults are expressed as a percentage of those estimated to have been alive during the previous summer, based on an assumed constant annual adult survival of 0.9 (see Results). Trends in recovery rates over years were analyzed by linear regression, using the multiple regression procedure of STATISTICA.

2.3 Counts of individuals on study plots

Ten count plots were selected in 1985 and their boundaries recorded on photographs and sketch maps. The plots were not selected at random but chosen for ease of visibility and distribution over the length of the colony. Five plots were adjacent to the upper edge of the colony, so their upper boundary was not defined, and new sites added at the upper margin were included as they were colonized (peripheral plots); the other five (central) plots were also situated in the top half of the colony, but were bounded on all sides by occupied areas (Gaston et al. 1993). The occupied area of cliffs at Coats Island is 12–85 m above sea level. Each plot was counted daily at 17:00–18:00, whenever observers were present at the colony.

Interyear comparisons for the period 1985–1999 were based on the mean of daily counts made between 1 and 7 August, a period when observers were present in every year. This is also the time in the season (early to mid chick rearing) when numbers of Thick-billed Murres counted at the colony tend to be most stable (Gaston and Nettleship 1981). Counts made when wind speeds exceeded 50 km/h were omitted because high winds tend to reduce attendance at the colony (Gaston and Nettleship 1981; AJG, unpubl. data).

2.4 Numbers of occupied breeding sites

Intensive observations of breeding biology were made for four breeding study plots (D, N, Q, S) from 1990 onwards. One of these plots (D) was also a count plot. Breeding sites were mapped on photographs and sketches of the study plots. Methods followed those of Birkhead and Nettleship (1980), with each site checked daily from a distance for the presence of an egg or chick. For analysis of trends in numbers of breeding pairs, only eggs laid on ledges that have been kept under observation annually since 1990, and where the whole ledge was visible to the observer (so that all increases and decreases would be detectable), were included. These restrictions meant that all of plots D and Q, but only parts of plots N and S, were included in the present analysis. Two areas on the periphery of the occupied cliff were colonized during the study, one adjacent to plot N (ledge N1) and one adjacent to plot D (area DA). In some analyses, these two, newly occupied areas were considered separately from those areas occupied from the beginning of the study.

2.5 Recruitment of first-time breeders

The majority of Thick-billed Murres begin to breed at 4–6 years of age (Gaston et al. 1994; de Forest and Gaston 1996). To examine the size of recruiting cohorts, I used the numbers of birds banded as chicks and known to be 4 and 5 years old observed on the breeding study plots each year; most of these birds were first-time breeders. Only those birds attending sites where an egg was known to have been laid were included. The representation of each cohort was expressed as a percentage of nestlings banded on the whole colony in that year.

2.6 Survival of breeding adults

A sample of breeding adults was banded on the breeding study plots each year from 1984 onwards. In 1984, banding was carried out with standard U.S. Fish and Wildlife Service stainless steel bands (number runs around a circular band); in 1985, all bands placed on breeders and half of those placed on nestlings were special triangular "murre bands" (designed by the British Trust for Ornithology) made from incoloy, with the number engraved upright on both sides of the band. The three-digit prefix was the same on all these bands, so only five digits needed to be read to reveal the complete number. From 1986 onwards, only the murre bands were used. Breeding birds were given a light-green plastic band above the metal band and a year-class colour on the other leg. Nestlings were given a year-class colour above the metal band. From 1995, additional numbered plastic bands, as well as a variety of different colour combinations, were placed on some birds. No evidence of band loss was observed for metal bands up to 1999. Bands removed after 12 years showed little signs of corrosion and required considerable force to open. Loss of metal bands is presumed to have been negligible.

Survival was estimated as the proportion of birds observed breeding in one year that were known to be alive the next year, whether breeding or not. All sites included in the survival sample were easy to observe, making the detection of bands close to 100%. However, numbers could not always be read completely, either because the bands were of the standard type (1984 banding) or because the characteristics of the site made the bands hard to see. If the colour and metal band combination was an unusual one and the same as that observed at the same site in the previous year, or if the partially read number, including at least three digits of the unique five-digit number, corresponded to the bird found at the same site the previous year, then the birds were considered to be the same individuals.

Although sites selected for inclusion in the survival analysis were chosen so that banded birds, if present, were almost certain to be detected, a few birds that were not recorded in a given year were seen in the next or subsequent years (3% of eligible cases). In about half of these cases, the reappearance was associated with a change of breeding site,

suggesting that nonsighting was often associated with abandonment of a breeding site. Presumably some birds that shifted sites moved to ledges not visible to us (of which there are many close to our study plots). If so, their disappearance constituted dispersal, rather than mortality, and the survival estimates must underestimate true survival to a small, but unknown, degree, the effect increasing with year (because in later years there were fewer subsequent years in which missing bands could have been rediscovered). The alteration in the probability of resightings associated with the high proportion of missing years that involved shifts of breeding site made these data ineligible for mark–recapture analysis (LeBreton et al. 1992). Earlier mark–recapture analysis for the same population suggested that the underestimate of survival estimates made by direct observation was of the order of 1% (Gaston et al. 1994).

3. Results

3.1 Banding recoveries

The proportion of birds banded as chicks at Coats Island that were recovered by hunters in Newfoundland in their first winter varied significantly among years ($\chi^2_{15} = 148$, $P < 0.001$), but no trend was discernible with year ($R^2 = 0.11$, $F_{1,13} = 2.71$, $P = 0.12$; Fig. 1). Mean annual recovery rates before 1993 (i.e., prior to the institution of new hunting restrictions) averaged 1.50%, and after 1993, 1.39% ($t = 0.24$, df 14, ns). Recoveries of second-year birds showed a significant negative trend with year ($\beta = -0.70$, $R^2 = 0.44$, $F_{1,12} = 11.41$, $P = 0.02$), as did recoveries of birds 3–6 years of age ($\beta = -0.77$, $R^2 = 0.53$, $F_{1,8} = 11.34$, $P < 0.01$). The three winters of lowest second-year recovery rates all occurred after 1993, as did two of the three lowest years for birds 3–6 years of age (Fig. 2; 1990 and 1991 cohorts). First-year recoveries aggregated into the same 4-year groupings used to estimate recovery rates of birds 3–6 years of age showed no trend with year ($R^2 = 0.00$, $F_{1,8} = 0.002$, ns).

Annual recovery rates of birds banded as adults ranged up to 1.5% (1985), but did not exceed 0.2% after 1990. Recovery rate showed a negative trend with year ($\beta = -0.66$, $R^2 = 0.39$, $F_{1,13} = 10.04$, $P < 0.01$). In fact, only five recoveries of birds banded as adults were reported after 1991 (overall mean recovery rate 0.07% for 7508 bird-years [1991–1998]; Fig. 3).

3.2 Counts of individuals on study plots

Mean numbers counted on the study plots during 1–7 August in 1985–1999 fluctuated from a low of 1509 ± 40 (SD) in 1991 to a high of 2080 ± 71 in 1997 (Fig. 4). Numbers increased significantly with year ($\beta = 0.71$, $R^2 = 0.47$, $F_{1,12} = 12.39$, $P < 0.01$), but the relationship was far from linear (see Gaston, this volume).

When central and peripheral plots were considered separately, there was a significant increasing trend for the peripheral plots ($\beta = 0.85$, $R^2 = 0.70$, $F_{1,12} = 31.13$, $P < 0.01$), but not for the central plots ($R^2 = 0.00$, $F_{1,12} = 0.47$, ns), although central plots fluctuated slightly, with year-to-year changes generally concordant with those on peripheral plots.

Figure 1
Percentage of first-year (1Y), second-year (2Y), and third-year (3Y) Thick-billed Murres recovered in Newfoundland and Labrador in relation to year of banding

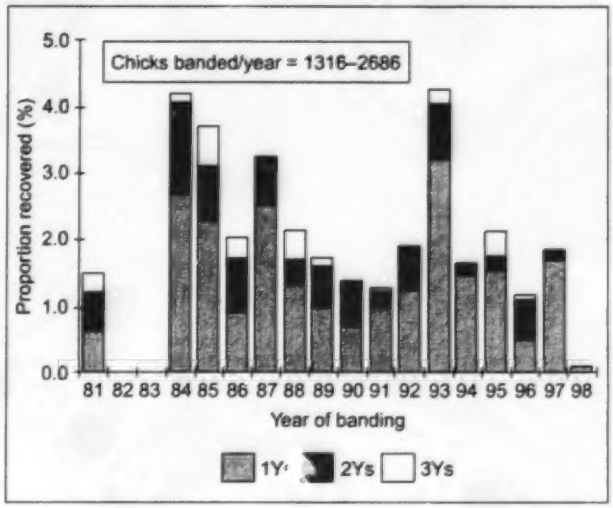
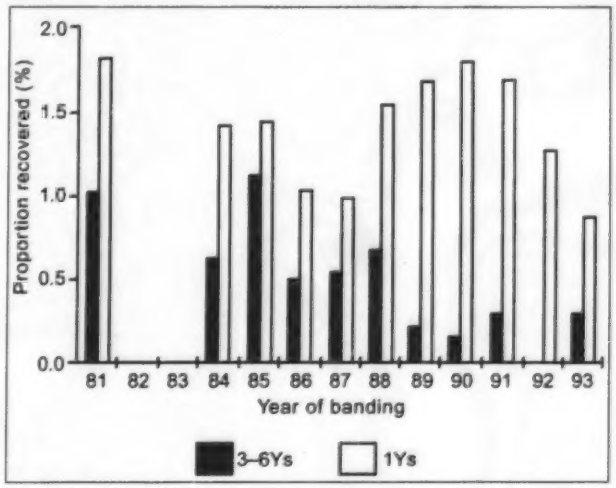


Figure 2
Percentage of 3- to 6-year-old Thick-billed Murres recovered in Newfoundland and Labrador in relation to year of banding, compared with first-year recoveries aggregated over the same 4-year periods



3.3 Numbers of breeding pairs

The lowest number of breeding pairs was recorded in 1991, when eggs were laid on 273 sites, and the highest in 1999, when eggs were laid on 480 sites. There was a significant increase in the number of breeding sites with year ($\beta = 0.90$, $R^2 = 0.79$, $F_{1,7} = 31.5$, $P < 0.01$). There was a sharp increase in the number of breeding pairs in 1994 (18%) and again in 1997 (21%). Most of the increases came through the occupation of additional ledges at the periphery of the occupied area (Fig. 5). In 1994, the main increase came through the addition of sites on ledge N1, where birds had been prospecting for several years previously. In 1997, the main increase came on area DA, where birds had been prospecting from 1993 onwards. It appears that sudden expansions occur when years of good feeding conditions allow

Figure 3
Annual recovery rates of Thick-billed Murres banded as adults and recovered in Newfoundland and Labrador, as a proportion of those estimated to be alive in each year (estimates given above bars)

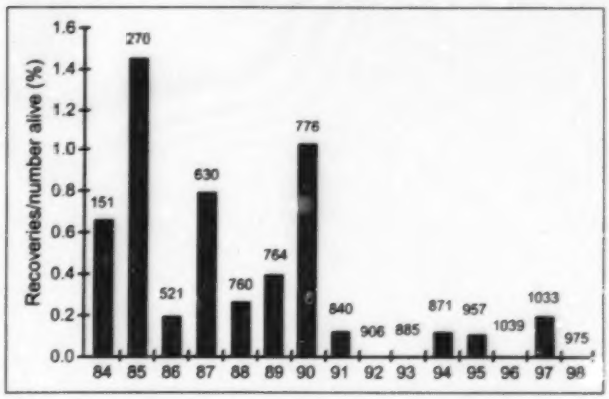


Figure 4
Trends in mean counts of adult Thick-billed Murres at sample plots on Coats

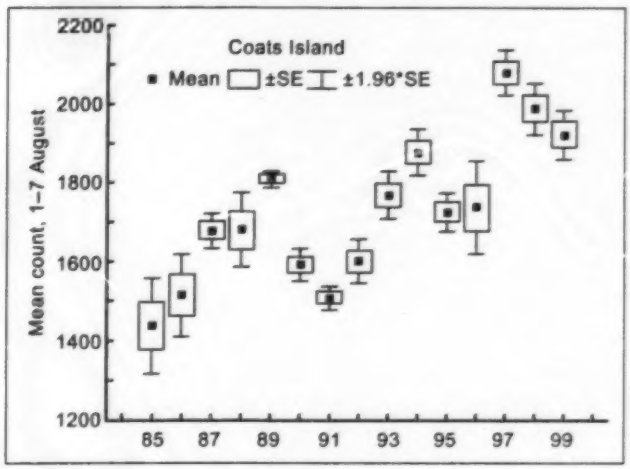
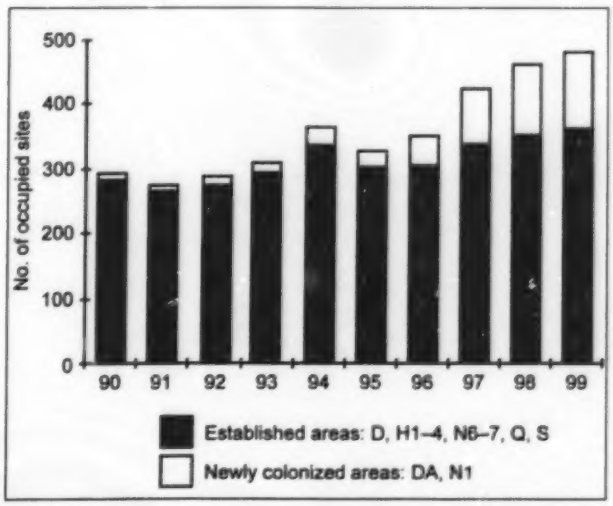


Figure 5
Changes in the number of occupied breeding sites on selected study plots at Coats Island



many first-time breeders to initiate reproduction. Both 1994 and 1997 were years when breeding was early (AJG, unpubl. data). The majority of birds of known age that colonized the expansion areas were 3- to 6-year-olds, many of which were breeding for the first time (G. Donaldson and AJG, unpubl. data).

Numbers of birds counted on peripheral plots and numbers of pairs breeding on study plots were positively correlated ($r_7 = 0.94$, $P < 0.01$). The slope of the log–log regression (1.01) did not differ significantly from 1, suggesting that the proportional increase in both variables was similar. Overall, there was a good concordance between year-on-year changes in mean counts on all plots and changes in the number of occupied sites (Fig. 6).

3.4 Recruitment of first-time breeders

The proportions of different cohorts that were found breeding on the study plots varied from 0.25 to 2.2% for 4-year-olds (4Y) and from 0.5 to 2.3% for 5-year-olds (5Y), with significant interyear variation ($\chi^2_{[4Y]} = 43.9$, df 9, $P < 0.01$; $\chi^2_{[5Y]} = 43.5$, df 9, $P < 0.01$). Recruitment was highest for both age classes in 1998 and lowest for 4-year-olds in 1993 and for 5-year-olds in 1996 (Fig. 7). The proportion of 4-year-olds increased significantly with year ($\beta = 0.65$, $R^2_{[4Y]} = 0.36$, $F_{1,8} = 6.01$, $P = 0.04$). The proportion of 5-year-olds also increased, but not significantly ($R^2_{[5Y]} = 0.22$, $F_{1,7} = 3.51$, ns).

Comparing proportions of recruits with banding recovery data, there was no significant correlation between the proportion of a cohort recovered in the first or second year in Newfoundland and its subsequent recruitment at either 4 or 5 years of age (all $P > 0.2$).

3.5 Survival rates

Annual survival rates of breeding adults varied from 0.85 to 0.93 and showed no significant trend with time ($R^2 = 0.01$, df 8, $P > 0.1$). There was no significant variation among years. Nor was there any correlation between the survival of breeders from one year to the next and the change in breeding numbers or counts over the same interval ($R^2 = 0.01$ and 0.04, respectively, df 7, $P > 0.1$). Combining all data for years before and after the 1993–1994 winter gave estimates of 0.90 (n = 585) and 0.89 (n = 663), respectively (not significantly different).

4. Discussion

4.1 Banding recoveries

Hunting of murres off Newfoundland and Labrador is carried out from small boats operating mainly within 5 km of shore. Anecdotal accounts by hunters suggest that the total harvest in a given area varies greatly from year to year in response to weather, sea, and ice conditions (Elliot 1991). Although total harvest over the whole province fluctuates less (Wendt and Cooch 1984; Chardine et al. 1999), it is likely that much of the interyear variation in recovery rates is caused by variation in hunting intensity relating to environmental factors.

Figure 6
The relationship between year-on-year changes in counts of birds present and changes in numbers of occupied breeding sites. Year labels refer to the second year of the comparison.

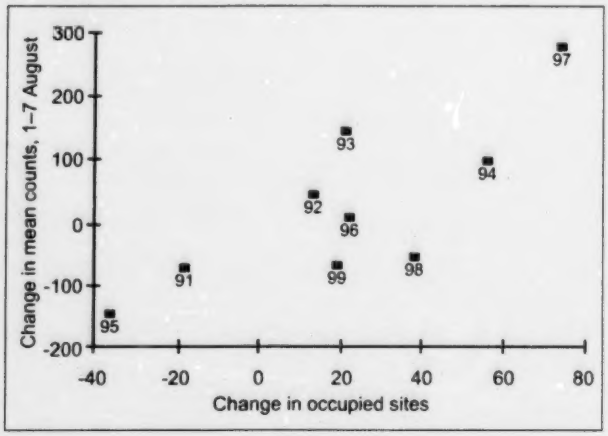
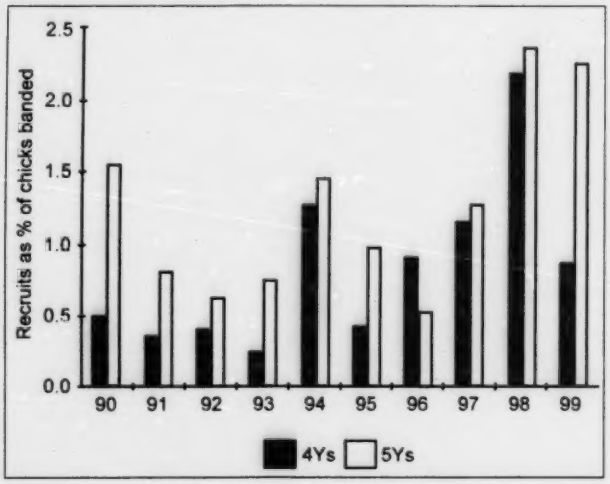


Figure 7
Trends in the proportions of 4- (4Y) and 5-year-old (5Y) murres breeding on the Coats Island study plots



Analysis of banding recoveries suggests that the magnitude of changes in recovery rates over time is linked to age. First-year recoveries showed no trend over time, but a negative linear regression with year explained 44% of variation in second-year recoveries and 53% for those in their third to sixth years. Recoveries of birds banded as breeders virtually ceased after 1990. Although some variation in reporting rates over the period of the study is likely, the lack of trend in first-year recoveries makes it unlikely that changes in reporting rates could have produced the observed patterns for other age groups. Moreover, in the winter of 2000–2001, several recoveries of breeding-age birds were received and few of first-years, suggesting a possible return to earlier conditions (AJG, unpubl. data).

Previous analyses of banding recoveries showed that, prior to 1993, first-year birds formed the majority of those harvested in October–December, and birds in their third year and older were recovered predominantly in January–March, with the peak coming in February. Second-year birds were intermediate, being harvested more or less throughout October–March, the period of the legal hunt (Elliot et al. 1990, 1991; Donaldson et al. 1997).

A change in age-specific recovery rates was anticipated when the hunting regulations were changed in 1993. By ending the hunting season on 10 March, instead of at the end of the month, it was hoped that the kill of breeding-age birds would be reduced more than that of younger age classes. Otherwise, the intention was to keep the proportion of the harvest in different areas and in different months approximately the same. This was done by allowing the season limits for each hunting zone to include the period of peak hunting for that area, which should have resulted in a uniform effect across age classes up to 10 March. Since 1993, harvests have been allowed up to 10 March on the south coast of Newfoundland, where a high proportion of recoveries of birds more than 2 years old occurred prior to 1990 (Donaldson et al. 1997).

Because closing hunting on 10 March was expected to reduce recoveries of breeding-age birds, it is likely that some of the change in age-specific recovery rates has been brought about by the change in regulations. However, the magnitude of the change for breeders (>90% reduction since 1990) and the fact that the most striking change in recovery rates for third-year and older birds occurred from 1990 onwards (before the imposition of current regulations) were not anticipated.

The lack of coincidence between changes in recovery rates for older birds and changes in regulations argues strongly that some phenomenon other than hunting pressure was responsible for most of the observed change in recovery rates. It is possible that there was a change in the wintering area of Coats Island Thick-billed Murres from 1990 onwards, the change being most marked for birds of breeding age. This change could have involved a relatively small displacement from inshore to offshore areas or a more radical change to wintering completely outside of Newfoundland waters. There is some anecdotal evidence to suggest that after 1990, many murres on the east coast of Newfoundland were feeding farther offshore than previously, but the distribution of different age groups was not known (J. Chardine, pers. commun.).

Recovery rates of first-year birds showed no change coincident with the imposition of hunting restrictions. If the introduction of bag limits meant that hunters limited their kill to the birds most easily shot, then we might expect an increase in the proportion of naive, first-year birds, relative to older age classes. This effect may account for the continuing high harvest of first-years. The lack of correlation between first-year recovery rates and subsequent changes in population parameters suggests that there may have been other important causes of first-year mortality that either swamped, or compensated for, those caused by hunting.

4.2 Observations at the breeding colonies

If hunting restrictions decreased the mortality of adult Thick-billed Murres from the winter of 1993–1994 onwards, we might have expected to see a contrast between the period before and after that winter. Of the data sets examined, only the number of breeding pairs on the study plots and the number of 4-year-old and 5-year-old recruits (these variables correlated) appeared to show such a contrast. Big increases in numbers of breeders occurred in 1994 (18%) and 1997

(21%), resulting in a 38% increase in the mean number of pairs breeding between 1990–1993 and 1994–1999. Likewise, recruitment of 4-year-olds during 1996–1999 was higher than in all but one earlier year, and recruitment of 5-year-olds in 1998 and 1999 was 55% and 47% higher than in any earlier year. There was no evidence that these changes were linked to reduced hunting mortality, as no correlations were found between recruitment of 4-year-olds or 5-year-olds and winter recovery rates for any age class.

Considering the period for which data on breeding sites were available (1990 onwards), the daily counts of study plots showed a trend similar to the trend in breeding sites, especially those on the peripheral plots (see also Gaston, this volume). The rate of increase in counts between 1985 and 1989 was somewhat more rapid than from 1991 onwards. Overall, the most striking changes in numbers of birds on the count plots were the decline between 1989 and 1990 and the sharp increase between 1996 and 1997. As the counts on peripheral plots from 1990 onwards were strongly correlated with numbers of breeding sites occupied, it seems likely that the earlier increases in the counts were also accompanied by an increase in the number of breeders. Hence, the evidence for any effect of the restrictions on hunting on overall population trend is weak. Changes after 1993 are better explained by the continuation of a general trend of increase that seems to have persisted at Coats Island, with periodic reversals, since at least 1972 (Gaston et al. 1993). Observations at the breeding colony at Digges Island, 300 km to the east of Coats Island, and at Prince Leopold Island, in the High Arctic, also suggested that there was no change in population trends as a result of the 1993 regulations (Gaston, this volume).

If the restrictions on hunting imposed from the winter of 1993–1994 onwards resulted in an improvement in survival for second-year birds, we should see this reflected in increased recruitment at the colony for the cohorts from 1992 (as second-years) and especially 1993 onwards. As most birds do not breed until they are 4 years of age or older (Gaston et al. 1994), we might expect to see a strong effect only from 1997 onwards. The surge in new breeding sites and counts between 1996 and 1997 may reflect a better survival of the post-1992 cohorts, but we shall need current recruitment levels to continue for several years before this explanation becomes convincing, because a similar sharp increase occurred between 1993 and 1994, too soon to have been caused by the change in hunting pressure.

4.3 Possible effects of environmental changes in the wintering area

The sharp decline in numbers of birds counted on the study plots that occurred between 1989 and 1990 coincided with the abrupt onset of cold water conditions off Newfoundland (Colbourne et al. 1997), leading to severe disruption of food webs on the Newfoundland shelf (Montevecchi and Myers 1996, 1997; Carscadden et al. 2001). Adult birds captured at Coats Island during incubation in 1990 and 1991 were much lighter than those caught in later years (Gaston and Hipfner 1998), suggesting that they may have been in poorer condition at the start of the breeding season. Although this evidence is only circumstantial, it suggests that environmental changes in the wintering area may have affected the numbers of birds at the colony, as well as their condition, in the following summer. Moreover, the changes in ecosystems in the wintering area correspond to the change in the recovery rates of birds more than 2 years old, which was noticeable from 1991 onwards. The increase in numbers of birds on the study plots between 1992 and 1994 coincided with a gradual reversal of the unusual oceanographic conditions, but coincident changes in the recovery rates of birds more than 2 years old were not reversed. It is possible that the pattern of wintering behaviour established during the difficult years of 1989–1990 persisted subsequently.

5. Conclusions

The restrictions on hunting introduced in the 1993–1994 winter represented a major regulatory intervention in the harvest of murres off Newfoundland, designed to reduce the numbers killed by approximately 50%. Despite the size of the former harvest and the impact that it had on population model predictions (J. Chardine, pers. commun.), the effects of the new hunting regulations were hard to discern, either from band recoveries or from observations at the Coats Island breeding colony. It appears that the change in regulations came a few years after a shift in the wintering behaviour of Thick-billed Murres from Coats Island had taken place, but at a time when the change had not been identified. Consequently, the reductions in harvest did not operate in the manner envisaged by the regulators, because birds of breeding age, which the regulations sought to protect, were no longer being hunted in large numbers. Given the lack of recoveries of breeding-age birds in Newfoundland during the 1990s, the lack of any indication of a change in the survival rates of breeding birds at Coats Island is not surprising: if they were not being hunted, the change in regulations was unlikely to affect them. However, there is circumstantial evidence that changes in regulations may have caused an increase in recruitment to the Coats Island colony, the effect being noticeable since 1997, when birds that had been reared after the change in regulations began to breed. This effect could have been created by a reduction in the hunting mortality of second-year and older birds, but I found no evidence for this.

Some fluctuations in numbers of murres observed at the Coats Island colony since 1985 may have been related to changes in marine ecosystems in the wintering area, although a longer data series, combined with surveys of winter distributions, would be necessary to determine this with confidence. Because of the long time scale of environmental fluctuations, we probably need to be very patient if we want to understand the role of environmental changes in the dynamics of this and other murre populations. In any case, the lack of response to major changes in hunting pressure suggests that winter hunting mortality was not a dominant factor in the population dynamics of the Coats Island murres during the period considered.

Acknowledgements

The following assisted with banding or observations at Coats Island: Karel Allard, Thomas Alogut, Anton Berto, Gwyllim Blackburn, Don Croll, Leah de Forest, Sandra Dickman, Garry Donaldson, Christine Eberl, Richard Elliot, John Geale, Grant Gilchrist, Mark Hipfner, Colleen Hyslop, Gabriella Ibarguchi, Christine James, Sue Johnson, Kaj

Kampp, Clint Kelly, Kara Lefevre, Debbie Martin, Elizabeth McLaren, Josiah Nakoolak, David Noble, Marco Passeri, Luc Pelletier, Sophia Perin, and Kerry Woo. Pierre Ryan and John Chardine, Atlantic Region, Canadian Wildlife Service, helped to obtain band recovery information. Thanks also go to Lynn Peplinski and the staff of the Science Institute of the Northwest Territories, later the Nunavut Research Institute, and the Polar Continental Shelf Project of Natural Resources Canada for providing logistical support for our field camp. Funding for this research came from the Canadian Wildlife Service, the Natural Sciences and Engineering Research Council of Canada, and the Northern Studies Training Program. Earlier drafts benefited from the comments of Rob Barrett, Peter Blancher, Hugh Boyd, David Cairns, John Chardine, and Grant Gilchrist.

Results of monitoring Thick-billed Murre populations in the eastern Canadian Arctic, 1976–2000

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Abstract

Trends in Thick-billed Murre *Uria lomvia* populations at several colonies in the eastern Canadian Arctic have been monitored for the past 25 years. The program has been intermittent, and only three out of 10 major colonies have been counted more than three times since 1975: Prince Leopold Island (Barrow Strait), Coats Island, and Digges Island (both in northern Hudson Bay). This paper analyzes information obtained by the monitoring program to date to evaluate the suitability of the methods used and the evidence for population trends. At each colony, monitoring counts were made daily at a fixed time of day for periods of 7 days or more, in some cases throughout the breeding season. Counts were made at 7–10 study plots containing about 200 birds, conveniently visible from the cliff top.

At Coats Island, mean daily counts were found to be well correlated with numbers of breeding pairs located on separate breeding study areas. Hence, the monitoring counts provide a useful index of the breeding population at that colony. Seasonal fluctuations in attendance patterns differed among colonies and also among years at the same colony; however, in most years at all three colonies, peak counts occurred in late July to mid-August, corresponding with the early part of the chick-rearing period. Fluctuations in numbers from day to day and variation in counts as a proportion of the highest counts for the year were lowest at this period, which appears to be the best for carrying out monitoring activities. Increases in total numbers present at monitoring plots over the period of observations were observed at Coats and Prince Leopold islands, but these were not continuous, and the numbers counted at both colonies seem to have fallen between 1989 and 1991 and to have levelled off after 1998. At Digges Island, where the overall increase was very small, there was some evidence that a decline might have occurred during 1985–1990.

The evidence of similarity in fluctuations at colonies as far apart as Coats and Prince Leopold islands suggests that population changes may be determined by events on the wintering grounds. Recommendations for improvements and extensions to the monitoring program are presented.

Résumé

Les tendances des populations du Guillemot de Brünnich (*Uria lomvia*) dans plusieurs colonies de l'Est de l'Arctique canadien ont fait l'objet d'une surveillance au cours des 25 dernières années. Le programme a été réalisé de façon intermittente, et seulement trois des dix colonies importantes ont été dénombrées plus de trois fois depuis 1975, soit celles de l'île Prince Leopold (dans le détroit de Barrows), de l'île Coats et de l'île Digges (toutes deux situées dans le Nord de la baie d'Hudson). Cet article analyse les renseignements obtenus dans le cadre du programme de surveillance jusqu'à ce jour afin d'évaluer la pertinence des méthodes utilisées ainsi que les indications sur les tendances de la population. Dans chaque colonie, des dénombrements à des fins de surveillance ont été effectués quotidiennement à une heure fixe de la journée pour des périodes de sept jours ou plus et, dans certains cas, pendant toute la saison de nidification. On a effectué des dénombrements dans sept à dix lieux d'étude où se trouvaient environ 200 oiseaux qui étaient faciles à voir à partir du haut de la falaise.

À l'île Coats, on a trouvé que les dénombrements quotidiens moyens correspondaient bien au nombre de couples nicheurs se trouvant dans différentes zones de nidification étudiées. Ainsi, les dénombrements à des fins de surveillance fournissent un indice utile de la population nicheuse de cette colonie. Les variations saisonnières des modèles de fréquentation étaient différentes d'une colonie à l'autre et d'une année à l'autre dans une même colonie. Toutefois, les dénombrements les plus importants avaient lieu de la fin juillet à la mi-août, la plupart des années dans les trois colonies, ce qui correspond au début de la période de l'élevage des oisillons. Les fluctuations du nombre de jour en jour et la variation des dénombrements, proportionnellement aux dénombrements les plus élevés au cours de l'année, étaient à leur plus bas niveau à cette période, laquelle semble être le moment le plus propice à la tenue des activités de surveillance. On a noté une augmentation du nombre total d'oiseaux présent dans les zones de surveillance lors des périodes d'observation à l'île Coats et à l'île Prince Leopold, mais cela n'a pas duré, et les dénombrements effectués dans les deux colonies semblent avoir diminué de 1989 à 1991, puis s'être stabilisés après 1998. À l'île Digges, où

l'augmentation globale était très faible, certaines indications semblent montrer qu'une diminution est peut-être survenue entre 1985 et 1990.

Les preuves de fluctuations semblables dans des colonies aussi éloignées que celles de l'île Coats et de l'île Prince Leopold suggèrent que les modifications de populations sont peut-être attribuables à des événements dans les aires d'hivernage. On présente donc des recommandations afin d'améliorer et de développer le programme de surveillance.

1. Introduction

Thick-billed Murres *Uria lomvia* breed in large numbers in the eastern Canadian Arctic, where they are the most abundant seabird in summer. Populations breeding in Hudson Strait, Hudson Bay, and Lancaster Sound and on the Canadian side of Davis Strait and Baffin Bay make up 16% of global and 22% of North Atlantic populations (Gaston and Hipfner 2000). Thick-billed Murres are the subject of a major harvest in their winter quarters off Newfoundland and Labrador (Elliot 1991; Elliot et al. 1991; Donaldson et al. 1997). In addition, populations in West Greenland have declined substantially over the past 50 years (Kampp et al. 1995). Alarm has also been expressed over potential declines in Canadian colonies (Evans and Nettleship 1985). As a result, over the past three decades, Thick-billed Murres have been the subject of considerable census and monitoring efforts by the Canadian Wildlife Service. This paper describes the evidence for population trends deriving from current monitoring efforts and evaluates the techniques employed.

Thick-billed Murres nest in very large colonies (generally from 50 000 to more than half a million birds) on precipitous sea cliffs. Consequently, they are difficult to count from the ground, and most colony censuses have been based on counts of birds from photographs taken either from the air or from boats (Birkhead and Nettleship 1980; Gaston et al. 1985; Chapdelaine et al. 1986; Falk and Kampp 1997). Such counts generally underestimate the number of birds present, because birds at the edge of ledges obscure others behind them, while birds facing away from the camera, so that their white underparts are invisible, are hard to see, especially in areas of shadow. These problems can be overcome, to some extent, by carrying out ground-truthing counts of selected areas simultaneous with the photography (e.g., Harris et al. 1983; Gaston et al. 1985, 1993). However, such ground truthing is not always possible, and even land-based observers will miss some birds. Moreover, photo-counts are very labour intensive and costly and hence cannot be performed often.

Because of the foregoing problems, only two of the 10 large breeding colonies of Thick-billed Murres in the eastern Canadian Arctic (Fig. 1) have been subjected to more than one complete census, and those (Hantzsch Island, Coats Island) were two of the smallest (Table 1). The results of the complete censuses suggest that numbers of Thick-billed Murres at Hantzsch Island remained stable through the 1970s, while those at Coats Island, East colony, roughly doubled between 1972 and 1990 (Gaston 1999). The Hantzsch Island colony is situated on a very small islet where birds nest densely on practically all cliffs. It is possible that this colony is limited by the availability of

Figure 1
Map showing the major Thick-billed Murre colonies in eastern Canada

breeding sites and that no further expansion is possible. This does not appear to be true at any of the other colonies.

Because complete censuses are difficult, time-consuming, and expensive, the Canadian Wildlife Service has chosen to track changes in Thick-billed Murre populations principally by monitoring sample study plots ("monitoring plots") on selected colonies. This technique was advocated by Birkhead and Nettleship (1980) and has been adopted by monitoring schemes in Greenland (Falk and Kampp 1997), Norway (Anker-Nilssen et al. 1996), and Alaska (Dragoo et al. 2000). It is routinely used to monitor Common Murres *Uria aalge*, a species with very similar breeding biology (Wanless et al. 1982; Harris et al. 1983; Piatt and McLagan 1987; Rothery et al. 1988; Hatch and Hatch 1989). The monitoring scheme reported here was among the earliest to be established for murre populations anywhere, and no detailed report of the results has been presented previously, although some results were reported by Gaston et al. (1993) and Gaston (1999).

2. Methods

Because murres make no nest, incubating their single egg on the bare rock ledge, it is not possible to distinguish breeding birds from nonbreeders that may simply be occupying a site. Consequently, during counts, all birds present in the area are counted (following Birkhead and

Table 1
Current population estimates for Thick-billed Murre colonies in the eastern Canadian Arctic

Colony	Year of last census	Population (breeding pairs)	Trend since 1975[a]	Reference
Akpatok Island North[b]		?	?	*Chapdelaine et al. 1986*
Akpatok Island South	1982	120 000	?	Chapdelaine et al. 1986
Digges Sound[c]	1980	300 000	+	Gaston et al. 1985
Coats Island	1990	30 000	+	Gaston et al. 1993
Hantzsch Island	1982	50 000	s	Gaston 1991
The Minarets	1985	130 000	?	Gaston and Smith 1987
Cape Graham Moore, Bylot Island		25 000	?	Browne et al. 1975
Cape Hay, Bylot Island	1976	140 000	?	Birkhead and Nettleship 1980
Prince Leopold Island[d]	1975–1976	86 000	++	Gaston and Nettleship 1981
Coburg Island	1980	160 000	?	D.N. Nettleship and S. Tingley, unpubl. data

[a] Trends: + = increase <1% per annum; ++ = increase >1% per annum; s = stable; ? = unknown.
[b] Estimated as 220 000 pairs in Chapdelaine et al. (1986), but this number was based on uncorrected photo-counts and is now regarded as a severe underestimate.
[c] Digges Sound is the combined total of pairs breeding on East Digges Island and on the facing shores of the Ungava Peninsula (Cape Wolstenholme southwards).
[d] Part of the estimate was based on counts of photographs that were somewhat affected by fog. The total is certainly an underestimate and probably is better rounded to 100 000 pairs.

Nettleship 1980; Gaston and Nettleship 1981). This number will always be higher than the actual number of breeding sites, but is usually lower than the total number of breeding birds, as off-duty birds spend most of their time at sea. Data on changes in numbers of breeding sites and numbers of birds counted on study plots at Coats Island show that total numbers counted and numbers of breeding pairs present are strongly correlated (see Results).

In order to estimate total population size, numbers of murres counted need to be converted to numbers of breeding pairs or breeding individuals. The ratio of breeding pairs to number of birds counted ("k") is known to vary among colonies (Chapdelaine et al. 1986; Hatch and Hatch 1989; Gaston et al. 1993). It also varies with time of day, with time of year, and with any other variable that affects the numbers of nonbreeding birds or off-duty breeders that are present on the cliffs. To use monitoring counts as an index of population, it is necessary to assume that the average value of k for a given date and time remains more or less constant over many years. If k is assumed to be constant for a given colony, there is no value in converting monitoring counts to breeding pairs, because trends will be the same whether individual birds or pairs are considered. For the most part, I have confined my analyses and discussions to uncorrected counts.

2.1 Selection of study plots

Monitoring plots were chosen to support approximately 100 breeding pairs and selected from among areas where the murres could be easily counted under most weather conditions. Plots were spread out along the colony as far as possible commensurate with the ability of a single well-trained observer to count all plots within the space of 1 hour. At all colonies, the plots were outlined on photographs and sketch maps, and the points from which counts were made were marked with cairns or blinds (Gaston et al. 1987).

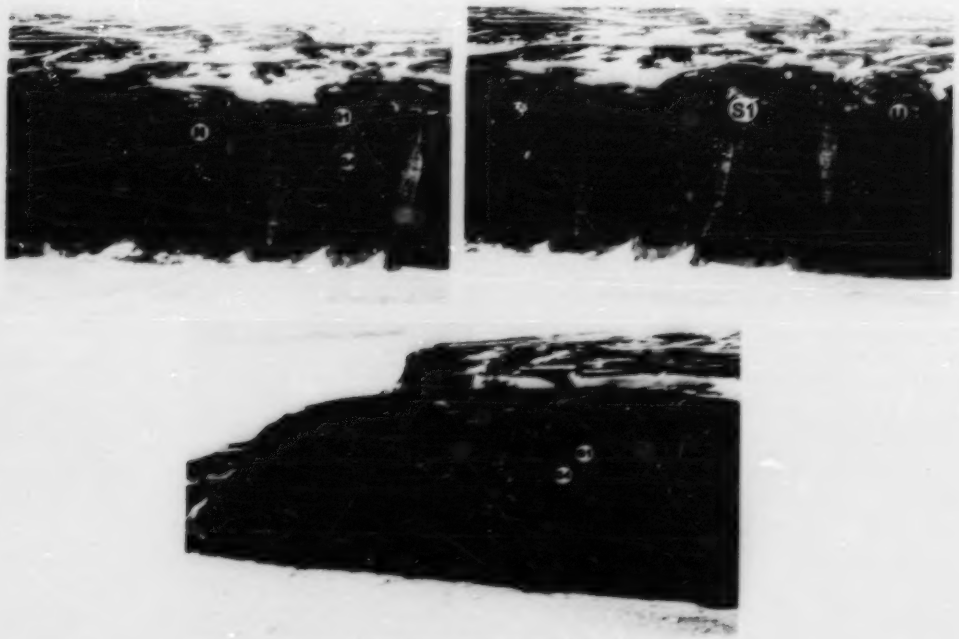
At Prince Leopold Island, murres breed in two aggregations, on the East Cliffs and beside the North Spit. For logistical reasons, all monitoring plots were situated on the East Cliffs colony, which contains approximately 80% of the Thick-billed Murres breeding on the island (Gaston and Nettleship 1981). Prince Leopold Island was the first colony where monitoring was implemented. Initially, 15 plots were selected, but eight were subsequently dropped because they were either too far from the observation point or too close to other plots. The remaining plots were spread over about 1.5 km. Because of the deep indentations in the cliff top at Prince Leopold Island, most observation points were situated so that the plots were more or less perpendicular to the direction of observation, a condition that made it easy to define the plot boundaries precisely.

Although chosen mainly for ease of observation from the cliff top, the plots at Prince Leopold Island were selected to include all types of breeding site (slope, aspect, ledge width, etc.). Hence, they were not a random sample, even of areas considered countable. Inevitably, they were biased towards areas near the top of the cliff, as these are closest to potential observation points. These selection procedures were not ideal, but were considered the only practical arrangement, given that fog frequently prevented the counting of distant areas.

The Coats Island colony comprises two subcolonies that support similar numbers of murres, separated by 1.5 km of unoccupied coast (Gaston et al. 1993). All plots were sited on the West colony, where visibility was better, and were spread over about 400 m. Because the cliffs at Coats Island are lower than those at Prince Leopold Island, not all plots had to be situated at the top of the colony, but some of those that were proved later to be situated in areas colonized within the past two decades (Gaston et al. 1993). These areas support a higher proportion of nonbreeding birds than those in the centre of the colony (AJG, unpubl. data). Because the cliffs have few indentations, and these only rather shallow, some plots had to be viewed at an oblique angle, making it more difficult to identify the boundaries than at Prince Leopold Island.

At Digges Island, the cliffs are 200 m high, again making it necessary to select plots near the top of the cliffs. A lack of indentations, and the fact that the cliff edge is covered by treacherous moss in many places, meant that several plots had to be placed close together. Overall, the plots were spread over about 1 km. The positions of all current Thick-billed Murre monitoring plots at the three

Figure 2
Position of monitoring plots at Prince Leopold Island



Prince Leopold Island, East Cliffs colony

colonies are shown in Figures 2–4. Individual plots are illustrated in Appendix 1.

At all three colonies, the boundaries of the monitoring plots were defined by natural features, such as vertical cracks, and areas of cliff without ledges, which excluded colonization by murres. At Prince Leopold Island, most plot boundaries were drawn to encompass discrete groups of murres, separated from neighbouring groups by areas of unoccupied cliff. In some cases, the plot boundaries were drawn very close to the margins of the groups of murres, so that subsequent expansions of the occupied area quickly exceeded the original boundaries of the plot. Because the original boundaries were drawn to delineate discrete groups, a decision was made to include the expansion areas, on the grounds that they would have been included if occupied originally. These plot expansions are shown in Appendix 1. If the discrete groups eventually coalesce with others, it may become difficult to define the exact plot boundary.

At Digges Island, and to a greater extent at Coats Island, where the cliffs were densely occupied, most of the monitoring plots were not discrete, and deciding whether a bird was "in" or "out" was sometimes a problem. At Coats Island, monitoring plots were classified as either "peripheral" (uppermost breeding sites forming the upper boundary of the occupied area — plots A, C, D, E, and G) or "central" (uppermost birds not at the upper boundary of the colony — all other plots). The upper boundary of the peripheral plots was not defined, so subsequent upward expansion of these plots, which has occurred at all but plot G, was automatically included within the count area.

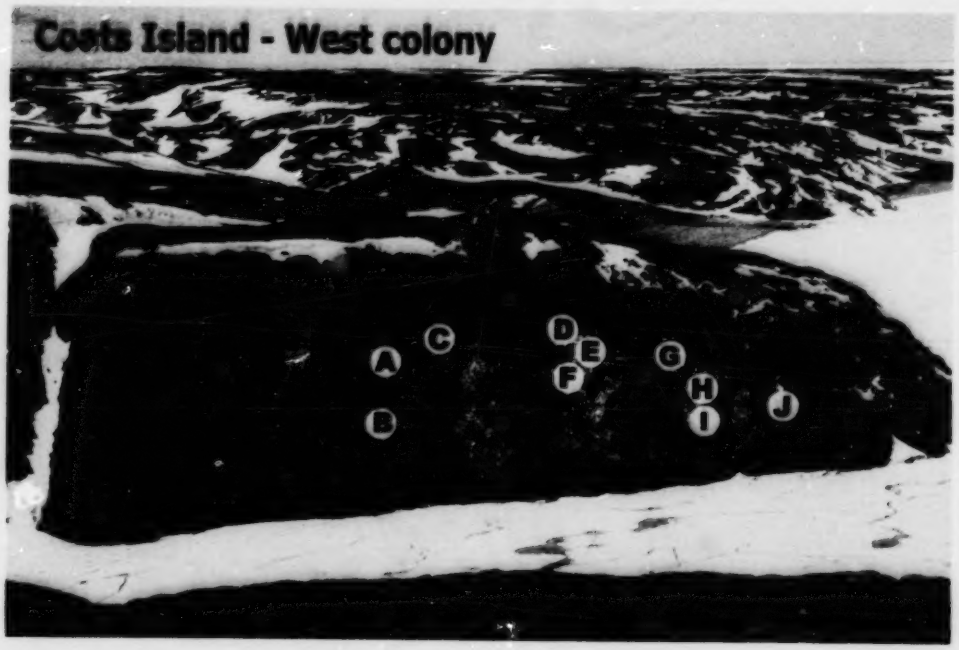
2.2 Counting procedures

The number of birds present on each monitoring plot was counted daily. All birds within the prescribed boundary were counted, even if only a small part could be seen (head, wing tip, etc.). This was considered less susceptible to differences of interpretation than any criterion relating to the proportion of a bird that was visible. Counts were made at a fixed time of day (17:00–19:00 Eastern Daylight Time at Digges and Coats islands; 17:00–19:00 Central Daylight Time at Prince Leopold Island). Previous studies of attendance patterns in relation to time of day suggest that, for Arctic-breeding Thick-billed Murres, time of day has little effect on attendance, except when light conditions are too poor to allow monitoring plots to be counted effectively (Gaston and Nettleship 1981; Gaston et al. 1985; Hatch and Hatch 1989). Consequently, this study does not address the effects of time of day.

Most counts were made by a single observer, using binoculars and a hand counter. Larger plots were generally counted in sections. Counts were repeated until successive counts were within ±5 birds (at most plots, this criterion was close to the ±3% recommended by Harris et al. [1983], but was easier to apply). The final count recorded was the mean of the two closest counts. Once experienced, observers seldom had to count more than twice to achieve consistency. However, under adverse weather conditions (e.g., rain blowing in the observer's face), several counts were necessary, even for experienced observers. New observers were checked by experienced observers for several days before counting on their own.

Figure 3
Position of monitoring plots at Digges Island

Figure 4
Position of monitoring plots at Coats Island



2.3 Frequency of monitoring

Since 1975, monitoring of selected study plots has been carried out more than five times at only three colonies (Table 2). The number of days of counts varied among years and among colonies. At Prince Leopold Island, baseline studies of breeding biology were carried out in 1976 and 1977, with counts of 10 study plots being made daily throughout each season. Subsequent monitoring at Prince Leopold Island has made use of only seven of these plots. At

Table 2
Monitoring counts at Arctic Thick-billed Murre colonies since 1975

Year	Prince Leopold Island	Digges Island	Coats Island
1976	7 May – 10 September		
1977	2 June – 9 September		
1980	24 July – 3 August	28 June – 30 August	
1981		20 June – 1 September	
1982		14 June – 30 August	
1984	18 July – 1 August		
1985		21–26 July	31 July – 10 August
1986			24 July – 7 August
1987	30 July – 6 August		25 July – 17 August
1988	18 July – 8 August		13 June – 16 August
1989			29 July – 17 August
1990		6–15 July	28 May – 23 August
1991			14 June – 27 August
1992		11–21 August	14 June – 24 August
1993	25 June – 5 July	29 July – 14 August	17 July – 20 August
1994		23 July – 4 August	11 June – 22 August
1995			8 June – 4 September
1996			13 June – 20 August
1997			15 June – 15 August
1998	28 June – 4 July		20 June – 9 August
1999		25 July – 6 August	24 June – 14 August
2000	20 July – 17 August		28 July – 19 August

Digges Island, the same procedure was carried out in 1980–1982 at 10 monitoring plots. At Coats Island, 10 monitoring plots were selected in 1985, but breeding studies and daily counts throughout the season were not performed until 1990. In addition, one of the original plots was dropped in 1986, because of difficulty in counting it, and was replaced with another plot. Counts for the new plot for 1985 were extrapolated from those in 1986 to estimate total numbers present at all 10 plots in 1985.

Wind speed at the cliff top and approximately 50 m from the cliff edge was recorded at 18:00, using a hand-held anemometer. Data on timing of breeding were derived from Gaston and Nettleship (1981) for Prince Leopold Island, from Gaston et al. (1985) for Digges Island, and from Gaston and Hipfner (1998) and additional unpublished data for Coats Island. The references give details of methods employed.

2.4 Interyear comparisons

The sums of all plot counts for a given date were used in interyear comparisons. For statistical analyses, I used the General Linear Model (GLM) program of STATISTICA (StatSoft, 1999) to derive a main effects model that partitioned variance due to date and year. The *post hoc* Newman-Keuls test was used to identify significant interyear differences. Annual rates of change in numbers were estimated by least-squares regression of annual means, log transformed, on year, using date as a covariate. Only dates between 20 June and 19 August were included in these calculations, as day-to-day variation in attendance increased substantially outside these limits.

To facilitate visual comparisons, some results are presented as a monitoring index derived from the ratio of counts in a given year to those made at the same dates in a baseline period (Coats Island, 1990; Prince Leopold Island, mean of 1976–1977; Digges Island, mean of 1980–1982). The mean of the sum of monitoring plot counts for each date was used as the baseline total count for that date and assigned an index value of 100.

As fog sometimes obscured some plots and not others, there were many days, especially at Prince Leopold Island, when one or more plot counts were missed. If only a single plot count was missing, the daily total was interpolated by:

$$C_{yt(\text{corrected})} = C_{yt} * C_{yt-1}/(C_{yt-1} - m)$$

where C_{yt-1} is the total count for the day before or day after, when all plots were counted, and m is the count on day t–1 for the plot that could not be counted on day t. If counts were missing for more than one plot, no C_{yt} was calculated for that day. Counts made on days when wind speeds at 18:00 exceeded 50 km/h were also omitted. The number of interpolated counts did not exceed 10% in any colony-year.

Previous analyses of changes in numbers at Coats Island (Gaston et al. 1993; Gaston 1999) were based on counts made during 1–7 August, a period in the middle of chick rearing, when numbers of adults tend to be at their most stable, and for which counts from every year are available. The results presented here, derived from the GLM analysis, yield similar results, but allow much additional information to be incorporated.

2.5 Autocorrelation among successive counts

To test for whether counts on successive days tended to be more similar than counts made several days apart, I used the partial autocorrelation program of STATISTICA, which corrects the correlation between counts separated by a lag of x days for correlations with the intervening days. I tested counts at Coats Island for the years when they were

available throughout the season (1988, 1990–1992, and 1994–1999).

2.6 Comparison with numbers of breeding sites

At Coats Island, from 1990 to 1999, intensive studies of breeding biology were carried out, using methods described by Birkhead and Nettleship (1980), at four study plots (D, N, Q, and S), one of which (D) was also a monitoring plot. The study plots are described by de Forest and Gaston (1996). The numbers of breeding sites where an egg was known to have been laid were used as an estimate of the breeding population of each plot.

2.7 Trends within years

To facilitate comparisons of trends within years, among years, and among colonies, a 7-day running mean of C_{yt} was calculated for all 7-day periods containing at least 4 days when a valid C_{yt} could be calculated (see above). Daily values for the 7-day mean were then expressed as percentages of the highest daily mean. For this analysis, I considered only those years when counts were available at least from 1 July to 10 August: 10 years at Coats Island, two at Prince Leopold Island, and three at Digges Island.

2.8 Variation among counts

To examine interplot differences in count variability at Coats Island, the coefficient of variation (ratio of standard deviation to mean) of counts over a 7-day period during the period when counts are most stable (1–7 August) was estimated for each plot in each year from 1988 to 2000. The period was chosen in order to minimize the effects of within-season trends in counts (see Results). Variation was also expressed as the standard error (SE) and 95% confidence interval on the mean ($SE * t_{\alpha,1}$).

3. Results

3.1 Numbers counted

When originally selected, the monitoring plots contained 75–250 birds during seasonal peaks. Those at Prince Leopold Island contained a mean of 129 birds per plot during 1–7 August in 1976, for a total of 903 birds, representing 0.45% of the breeding population. Corresponding values for Digges Island and Coats Island are given in Table 3. Depending on how we define the colonies (Digges Island versus Digges Sound, Coats Island West colony versus the whole Coats Island colony), the initial samples varied from less than 0.3% to 5.5% of the breeding populations. Because of increases in the numbers counted over the period of the study, the largest plot at Prince Leopold Island in 2000 (plot N) averaged 332 birds during 1–7 August, while the largest at Coats Island (plot A) averaged 414 birds during the same period. As some of those plots that began with the lowest numbers have scarcely increased, the result has been that a few large plots have come to comprise an ever greater proportion of the total count (see below).

3.2 Seasonal changes in attendance patterns

Total plot counts for all three colonies are presented in Appendices 2–4. These include a small number of counts where one plot was estimated by interpolation (see Methods). Running means presented below were based on these figures.

Descriptions of early- and late-season fluctuations in numbers of murres attending the colony were published previously for Prince Leopold Island (Gaston and Nettleship 1981). At Digges Island, crews arrived only just before laying commenced, so no information was obtained on the prelaying period. At Coats Island, counts began at the start of colony attendance only in 1990 and extended to colony desertion only in 1995. In 1990, high attendance during the prelaying phase alternated with periods when the colony was completely deserted (Fig. 5). Peak counts during this period exceeded those made later in the season by up to 12%. The low counts on 3 and 28 July and 16 August in 1990 coincided with very strong gales that caused all birds except those incubating or brooding to leave the cliffs. These counts were omitted from calculations of 7-day running means and from interyear comparisons that use 1990 as the baseline. In 1995, attendance was monitored until 10 September, but only a small number of birds (<20) brooding chicks from replacement layings were present after 2 September.

At Coats Island, monitoring counts exceeded 50% of the annual peak continuously on average from 20 June (earliest 14 June in 1995, latest 25 June in 1990, 1999; Table 4). The date of peak 7-day mean occurred between 18 July and 11 August in different years, except in 1995, when it occurred on 4 July (only years with counts beginning before 1 July considered, N = 10). The mean date, excluding 1995, was 3 August, 41 days after the mean date of median laying for the same years; eight peaks fell between 31 July and 10 August. There was no significant correlation between the date of peak numbers and the median date of laying (r_s = 0.309, P = 0.385). Peak dates were slightly earlier at Digges Island (19 and 25 July, 2 August); at Prince Leopold Island (2 and 11 August), they were similar to those at Coats Island.

At Coats Island, counts at median egg laying (about 23 June) averaged 82% of the peak, rising rapidly to about 90% of peak in early July and remaining between 90 and 94% of peak level until 28 July, when they again increased to the highest level in the first week of August (Fig. 6). Numbers declined from 10 August onwards.

The average seasonal pattern at Coats Island, described above, masks substantial year-to-year variation. Three fairly divergent examples are shown in Figure 7. In 1992, numbers rose rapidly in late June and remained relatively high thereafter (>90% of peak) until early August, when they began to decline gradually. In 1996, the increase was much more gradual, not reaching a plateau until the end of July and not falling much until after the middle of August. In contrast, in 1999, numbers were high (>95% of peak) from late June to 20 July and then fell to 80% of peak by 10 August. Daily total monitoring plot counts in July were significantly correlated only among 15 out of a possible 45 combinations of years, while for nine combinations there was a significant negative correlation. Of the positive correlations, the value of R^2 was greater than 0.25 for only nine out of 45 cases. This suggests that overall trends for July were very weak or, if present, were masked by year-specific effects.

Table 3
Numbers of birds counted daily on the monitoring plots during the week of peak counts in the first year of monitoring

Colony	Year	Number of plots	Mean count (range)	Number of breeding pairs	Proportion (%) of breeding population
Prince Leopold Island	1976	7	129.0 (76–227)	100 000	0.45
Digges Island	1980	10	158.6 (82–246)	180 000	0.44
Digges Sound				300 000	0.26
Coats Island, West colony	1985	9[a]	165.3 (100–258)	15 000	5.51
Coats Island, both colonies				33 000	2.50

[a] Nine in 1985; one plot was added in 1986.

Figure 5
Daily monitoring plot totals recorded at Coats Island in 1990 and 1995

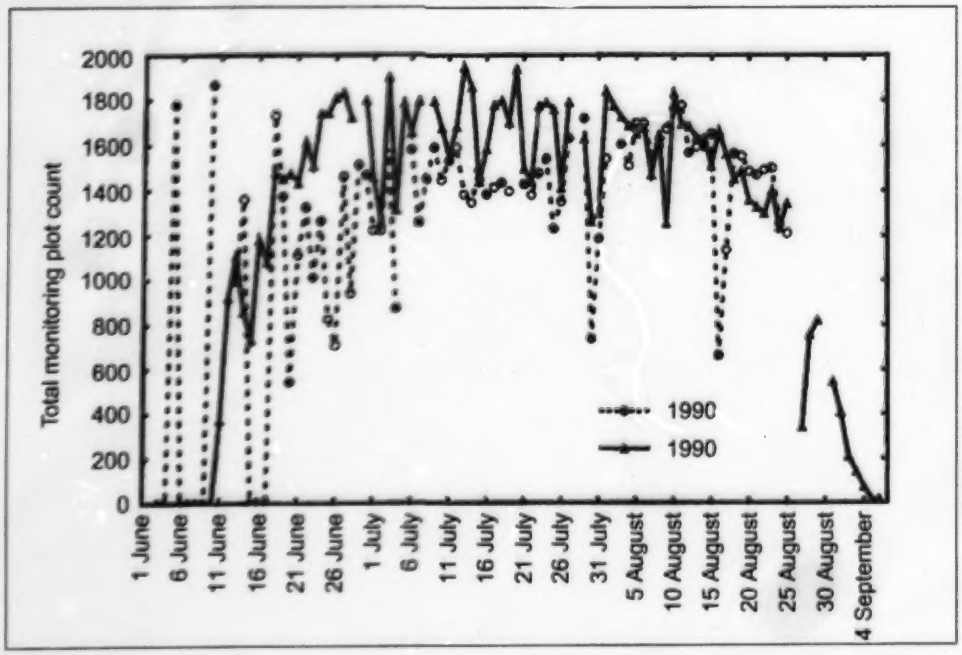


Table 4
Dates and attendance peaks at monitoring plots and counts in relation to timing of breeding at Coats Island

Year	Date after which counts did not fall below 50% of peak	Date of peak 7-day mean	7-day mean at median laying (% of peak)	7-day mean at median hatching (% of peak)	First date that counts fell below 90% of peak
1988	17 June	9 August	89.2	99.1	–
1990	25 June	10 August	69.7	79.1	17 August
1991	24 June	10 August	71.4	89.8	–
1992	23 June	1 August	90.0	98.4	19 August
1994	15 June	1 August	81.0	95.0	14 August
1995	14 June	4 July	91.0	93.9	4 August
1996	21 June	9 August	75.5	93.2	19 August
1997	–	31 July	81.3	94.0	–
1998	–	31 July	80.0	94.5	–
1999	25 June	18 July	89.0	87.8	3 August
Mean	20 June	3 August	81.8	92.4	13 August

Figure 6
Coats Island: 7-day means as percentage of yearly maxima, averaged over all years with full-season counts (1988–1999), with standard errors and 95% confidence intervals

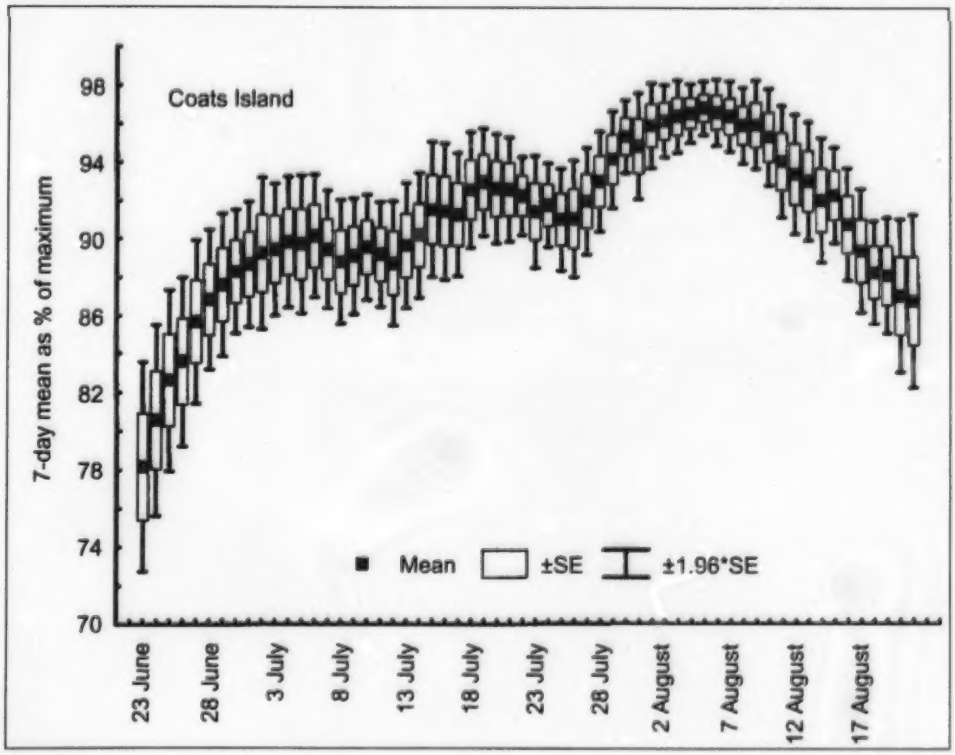


Figure 7
Coats Island: 7-day running means of monitoring plot totals for selected years (1992, 1996, 1999), showing interyear variation. Means are expressed as percentages of the highest 7-day mean for the year.

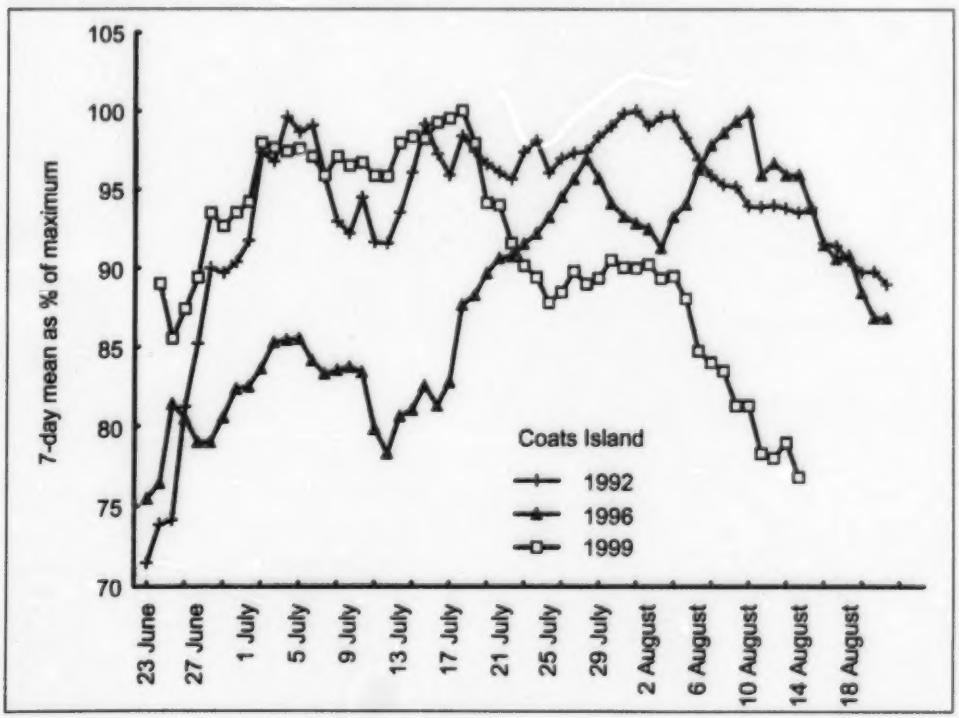


Figure 8
Digges Island: 7-day running means of monitoring plot totals for years with full-season counts. Means are expressed as percentages of the highest 7-day mean for the year.

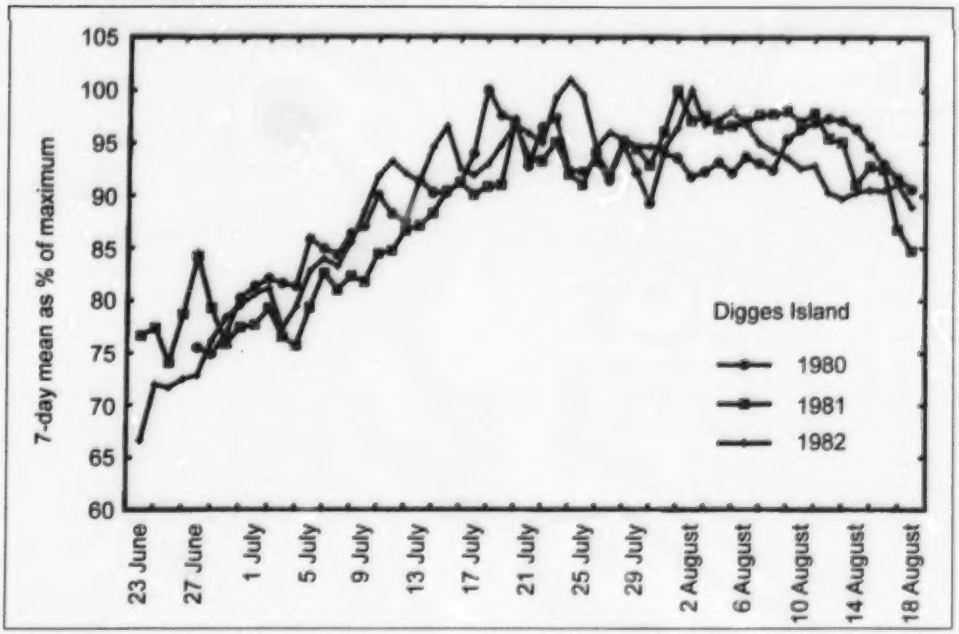
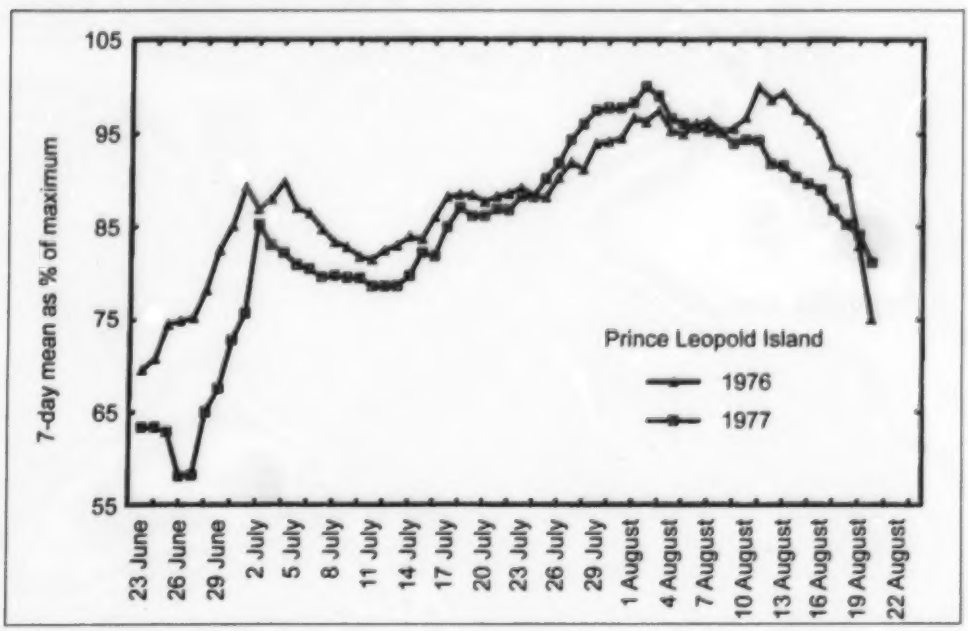
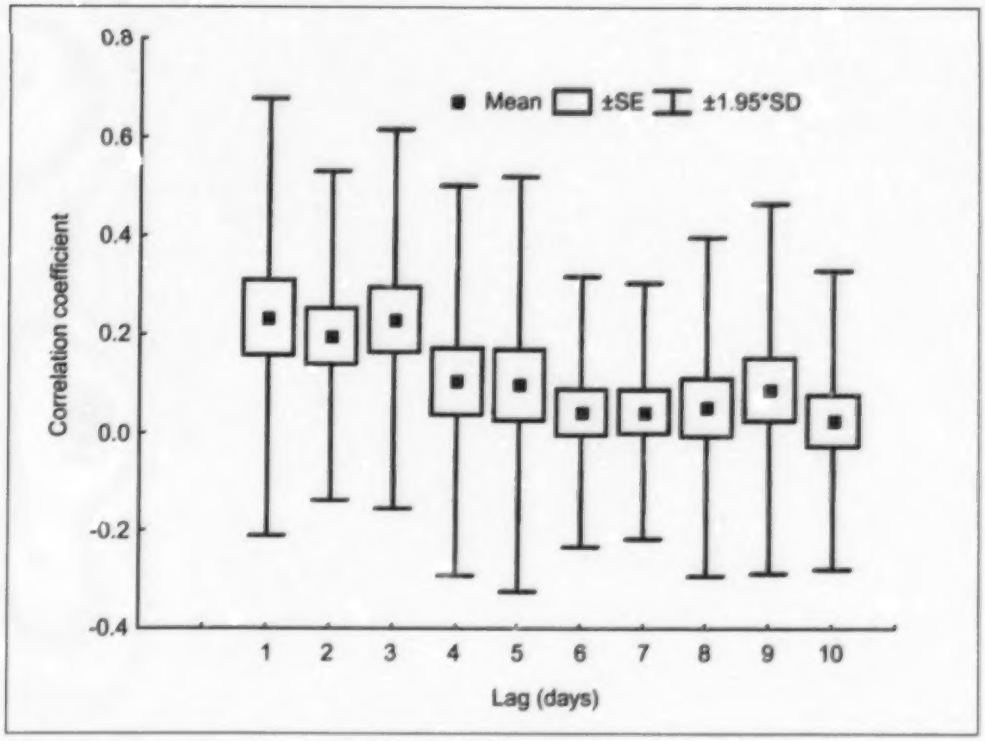


Figure 9
Prince Leopold Island: 7-day running means of monitoring plot totals for years with full-season counts. Means are expressed as percentages of the highest 7-day mean for the year.



At the other two colonies, the seasonal pattern in attendance differed strikingly from the one characteristic of Coats Island. At Digges Island, mean counts at median laying (average 28 June) were approximately 75% of peak and rose steadily, but more slowly than at Coats Island, levelling off after 20 July. Thereafter, they remained fairly stable until 10 August, after which they began to decline (Fig. 8). At Prince Leopold Island, in both years, numbers rose to a peak of 85–90% of maximum in early July, just after median date of laying, then fell to about 80% of maximum around 20 July and rose thereafter to the highest peak in early August (Fig. 9). Numbers did not begin to fall until 13 August in 1976, but fell from early August in 1977.

Figure 10
Mean values of partial autocorrelation analyses for counts at Coats Island in years when counts were made throughout the season.



3.3 Autocorrelation among counts

Significant autocorrelation among counts was found in some years, but not in others. No significant autocorrelations were found in 1994 and 1998 at lags of up to 10 days; in five other years, significant autocorrelation was found for only one or two lag periods, all but one within the first 3 days after the initial count. In 1997 and 1998, autocorrelation was significant at all lags up to 10 days. When the correlations for each lag period (1 day, 2 days, etc.) were averaged over all 9 years, only lags of 1, 2, and 3 days showed mean correlations above 0.1 (Fig. 10). Given that the occurrence of autocorrelation at lags of greater than 3 days was rare and that mean correlations even at lags less than 4 days did not exceed 0.3 (equivalent to $R^2 = 0.09$), autocorrelation was not considered to be an important factor in reducing variance and hence was not considered further.

3.4 Variation among counts

At Coats Island, interyear variation in 7-day means as a proportion of the highest 7-day mean for that year was lowest during the first 10 days of August (Fig. 6). This indicates that the relative counts were most predictable at that period, which corresponds roughly with the middle of the chick-rearing period, before chicks have begun to depart.

Variation in counts was higher in some years than in others. Taking the coefficients of variation for individual plots, the means were much higher in 1988, 1995, and 1996 than in other years (>10% compared with 8% or less) (Fig. 11; $F_{12,117} = 7.31$, $P < 0.001$). In addition, there was significant variation among plots when coefficients were averaged over years (Fig. 12; $F_{9,120} = 2.61$, $P = 0.009$), with variation highest at plots E and F, two plots at which numbers of murres increased rapidly between 1985 and 2000. There was no consistent correlation between mean coefficient of variation and mean count for a given plot, although in some years coefficient of variation was positively correlated with count (Rothery et al. [1988] reported a negative correlation for Common Murres). There was a significant positive correlation between the mean coefficient of variation for a given plot and the proportionate change in numbers over the period of the study (Fig. 13; $R^2 = 0.61$, $P = 0.008$). Although the coefficient of variation for all plots combined was higher than those for the two least variable plots, it was substantially lower than predicted by the regression on change in numbers, suggesting that the precision of the counts was improved by counting several plots.

At all three colonies, the mean confidence interval on the total counts for each date fell from approximately 30% of the mean count in mid-June to less than 10% after the median date of laying. This level was maintained until about 20 August, when it began to rise very steeply (Fig. 14), although variation tended to be a little higher at Digges Island than at the other two colonies. The most stable period was between 3 and 18 August, when the 95% confidence interval never exceeded 8% of the mean count at any colony.

3.5 Concordance among monitoring plots

At Coats Island, there was a general concordance between day-to-day changes at monitoring plots. Using

Figure 11
Coats Island monitoring plots: variation among years in coefficient of variation

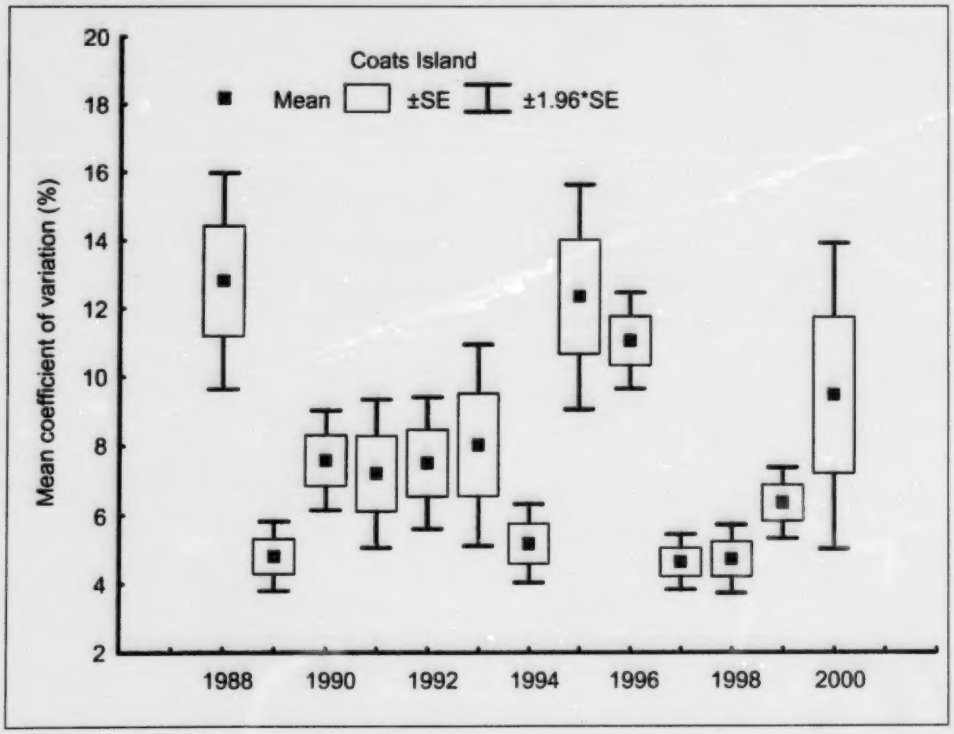


Figure 12
Coats Island monitoring plots: variation among plots in coefficient of variation

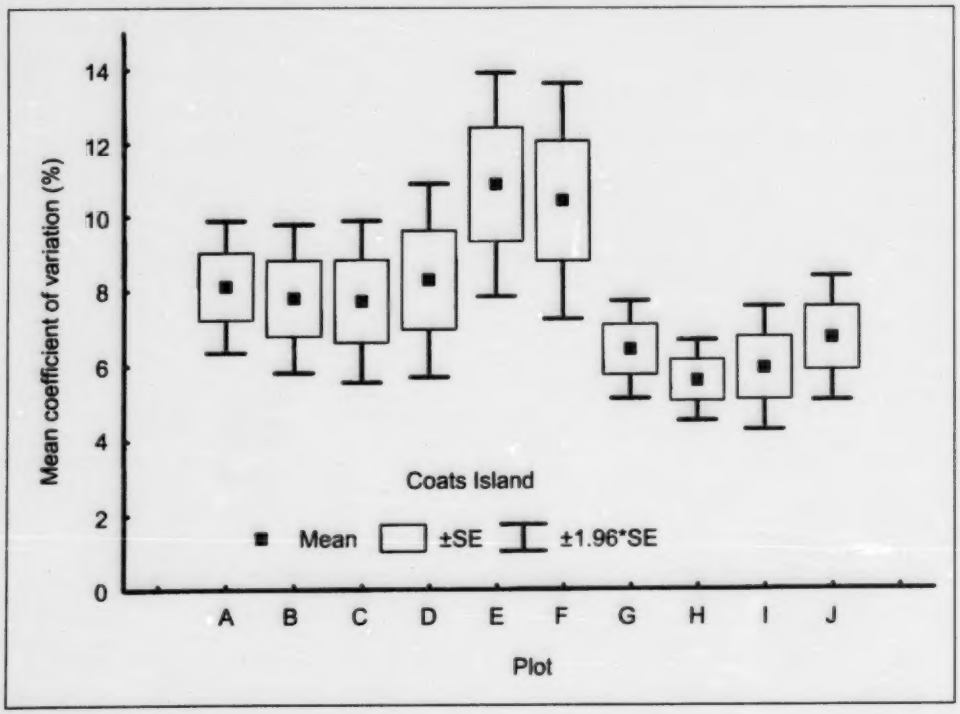


Figure 13
Coats Island monitoring plots: relationship between mean coefficients of variation and proportionate changes in numbers from 1985 to 2000. Dotted lines give 95% confidence bands on least-squares regression.

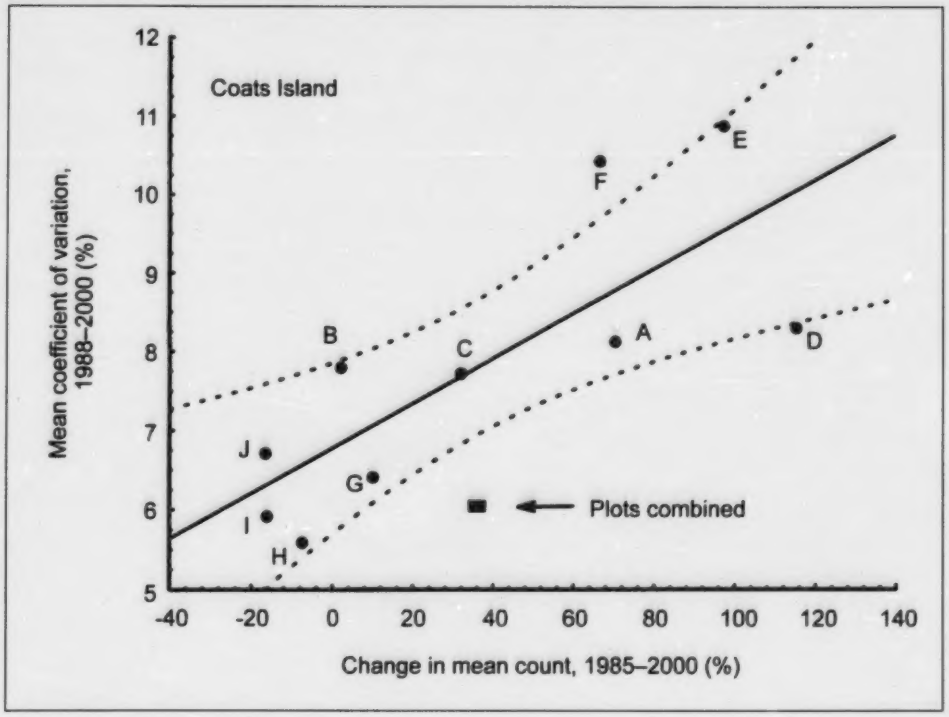


Figure 14
Seasonal change in the 95% confidence interval on the 7-day mean for the three colonies

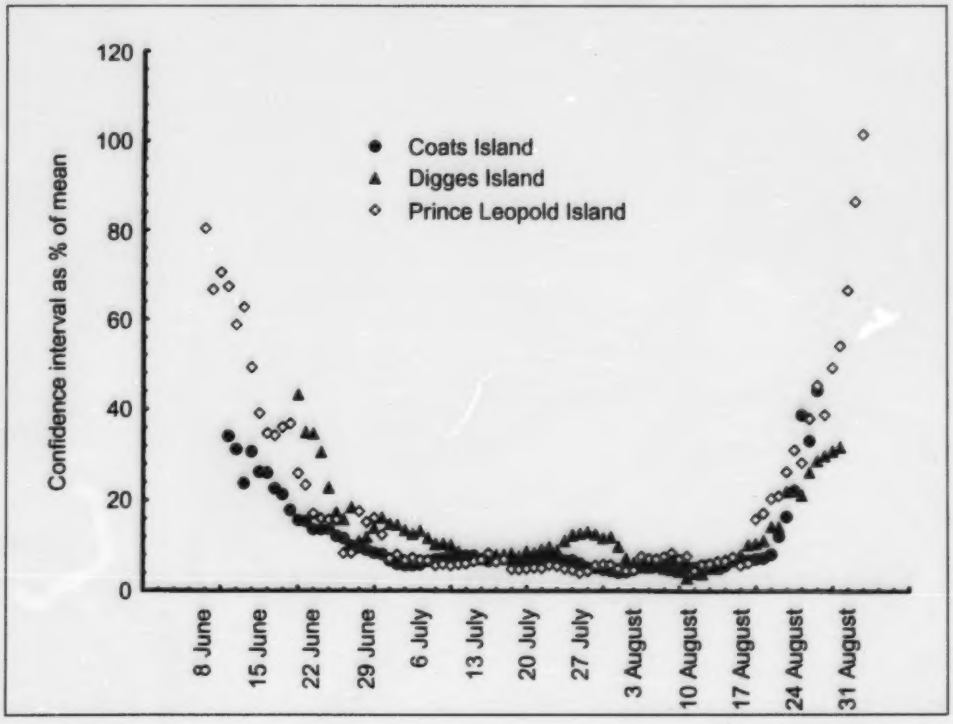
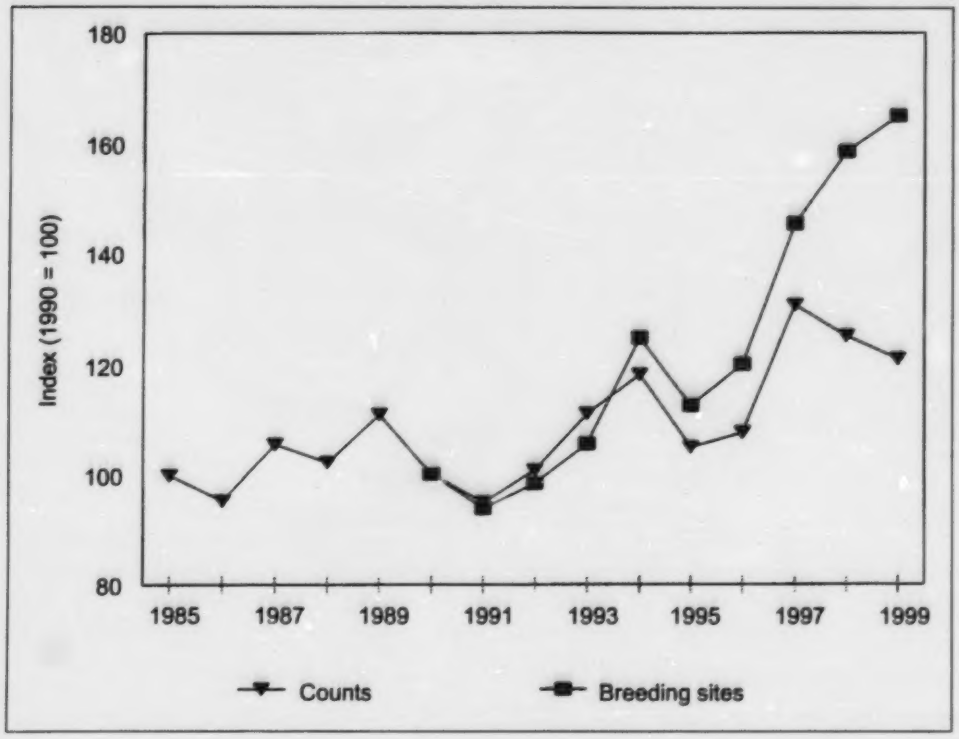


Figure 15
Comparison of monitoring counts for Coats Island with trends in the numbers of breeding sites on four study plots



counts for the month of July and the 10 years with counts for the entire month, 68% (N = 450) of correlations between pairs of plots were positive and significant.

The degree of concordance between plots varied with their relative positions on the colony. Three plots (A–C) are situated to the south of a steep gully that cuts through the centre of the colony; the rest (D–J) are to the north (Fig. 4). Comparing these two groups of plots, only 55% (N = 210) of correlations between them were positive and significant (mean $R^2 = 0.21$), compared with 63% (N = 30) of correlations among plots A–C (mean $R^2 = 0.23$) and 80% (N = 210) of correlations among plots D–J (mean $R^2 = 0.33$) (comparing the proportion of significant positive correlations among plots D–J with those between A–C and D–J, $\chi^2 = 27.1$, $P < 0.001$). Among plots D, E, and F, situated close together, facing in the same direction, and slightly isolated from the rest of the colony, all correlations (N = 30) were positive and significant in every year (mean $R^2 = 0.51$).

3.6 Comparison of monitoring plots with breeding sites

Monitoring counts and numbers of breeding sites were strongly correlated at Coats Island ($R^2 = 0.88$, $F_{1,8} = 66.8$, $P < 0.001$). The correlation for plot D, the only plot where both monitoring counts and breeding studies were performed, was similar ($R^2 = 0.83$, $F_{1,8} = 40.0$, $P < 0.001$). The two variables diverged somewhat after 1997, with breeding sites continuing to increase while monitoring plot counts levelled off (Fig. 15).

3.7 Population trends

Total monitoring plot counts increased at all three colonies during the periods of observation. Mean counts at Prince Leopold Island in 2000 were significantly higher than in 1976 and 1977 at all but one plot (Q4). At Coats Island, monitoring plot counts in 2000 were higher than those in 1985 at seven out of 10 plots and higher than those in 1990 at all plots (significantly at six plots). Monitoring plot counts at Digges Island in 1999 were higher than those in 1982 at nine out of 10 plots and significantly higher at seven.

At Prince Leopold Island, monitoring plot counts showed an average rate of increase, based on the regression slope of the combined total, of about 1.5% annually over the period of observations ($r_s = 0.89$, $P < 0.01$). Using the mean rate of increase averaged over individual study plots, the mean rate of change was the same. Corresponding figures for Digges Island were +0.4% for the combined total ($r_s = 0.47$, ns) and for the means of rates for individual plots. At Coats Island, the slope of the regression for the period 1985–2000 showed an annual rate of increase of 2.1% ($r_{15} = 0.83$, $P < 0.01$).

Rates of change averaged over the whole monitoring period obscure the fact that the rate of change varied from year to year both in magnitude and in direction. At Coats Island, counts increased from 1985 to 1989, fell sharply between 1989 and 1991, increased to 1994, fell again to 1996, and then rose sharply in 1997, remaining fairly stable since then (Fig. 16, Table 5). The increase from 1986 to 1989 was 26% (average +8.0% per annum), and from 1991 to 1994, 27% (average +8.4% per annum). The increase

Figure 16
Means and standard errors of monitoring indices at Coats Island during 1985–2000. Means are corrected for date using the least-squares method of the STATISTICA GLM procedure with date as a covariate (covariate mean = 23 July).

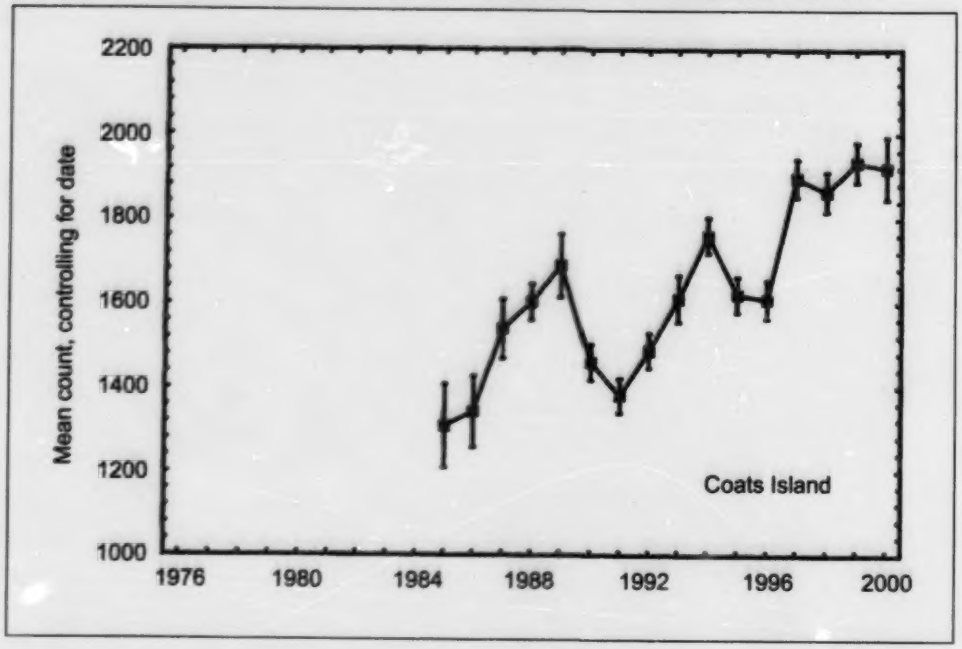


Table 5
Results of Newman-Keuls tests for retrospective differences among mean annual counts, controlled for the effect of date[a]

Year	Prince Leopold Island	Digges Island	Coats Island
1976	|		
1977	|		
1978			
1979			
1980	|	|	
1981		| |	
1982		| |	
1983			
1984	|		
1985		|	|
1986			|
1987	| |		|
1988	|		|
1989			|
1990		|	|
1991			|
1992		| | |	|
1993	|	| | |	|
1994		| | |	|
1995			|
1996			|
1997			|
1998	|		|
1999		| |	|
2000	|		|

[a] Years connected by vertical bars did not differ significantly; all other combinations were significantly different ($P < 0.05$). ANOVA results: Prince Leopold Island, $F_8 = 52.0$, $P < 0.001$; Digges Island, $F_8 = 5.5$, $P < 0.001$; Coats Island, $F_{15} = 52.2$, $P < 0.001$.

between 1993 and 1998 was 16% (+3.0% per annum), and between 1990 and 1999, 32% (+3.2% per annum).

Changes in the mean counts at Prince Leopold Island suggest an increase between the mid-1970s and 1980, followed by a decrease to 1984 and a sharp increase to 1988 (Fig. 17, Table 5). In 1993, numbers were lower than in 1988, but counts were made very early in the season (25 June – 5 July) in a year when laying was late (starting on 30 June) and variability in counts was very high. Counts in 1998 and 2000 were similar and higher than in 1988 and 1993. The increase between 1984 and 1987 was 15% (average +4.7% per annum), and between 1993 and 1998, 29% (+5.2% per annum).

At Digges Island, counts rose between 1980–1982 and 1985, were lower in 1990, returned to the 1985 level in 1992–1994, and were slightly higher in 1999 (Fig. 18). The most rapid increase occurred between 1990 and 1999, when numbers increased by 17% (average +1.7% per annum).

Comparing the trends in counts for the three colonies, counts at all colonies were significantly higher during the most recent counts than they were in the earliest years. Counts at both Coats Island and Prince Leopold Island increased sharply between 1984 and 1988 (Fig. 19). Counts at both colonies were at a very similar level in 1993 relative to those in 1988, increased to approximately the same extent between 1993 and 1998, and then remained at more or less the same level in 2000. Counts at Digges Island, which showed much smaller year-to-year variation than the other two colonies, resembled the others mainly in reaching their lowest level in 1990.

3.8 Variation in trends among plots

Despite the overall tendency to increase, the magnitude of change varied greatly within colonies; counts on

Figure 17
Means and standard errors of monitoring indices at Prince Leopold Island during 1976–2000. Means are corrected for date using the least-squares method of the STATISTICA GLM procedure with date as a covariate (covariate mean = 23 July).

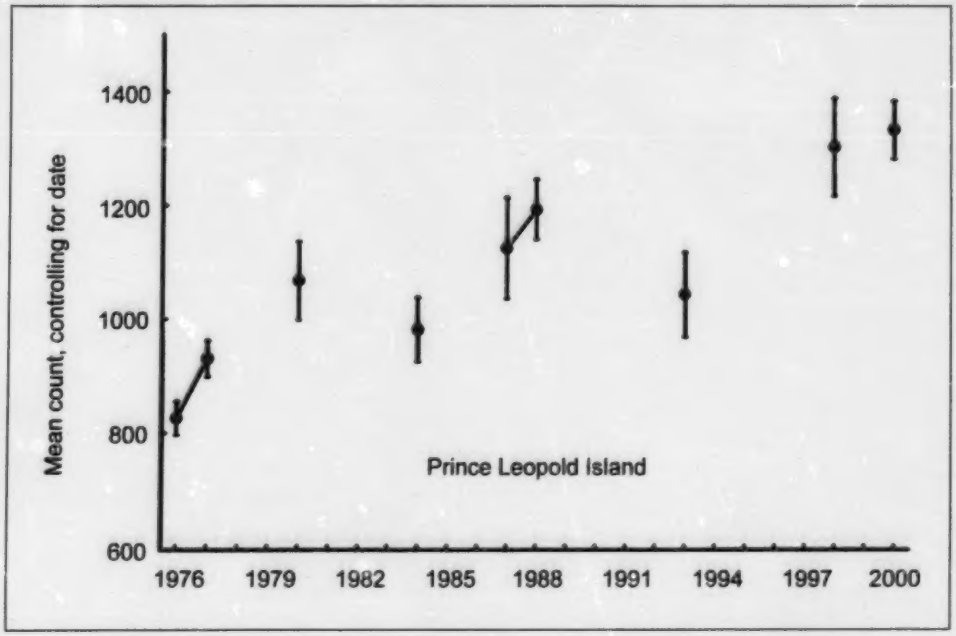


Figure 18
Means and standard errors of monitoring indices at Digges Island during 1980–1999. Means are corrected for date using the least-squares method of the STATISTICA GLM procedure with date as a covariate (covariate mean = 25 July).

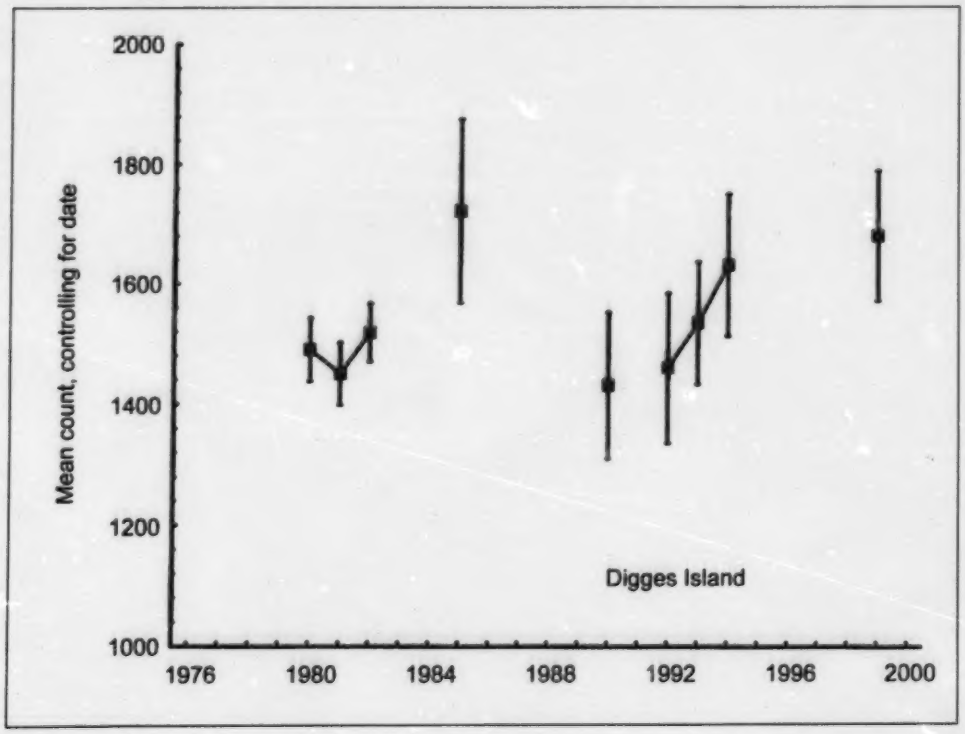
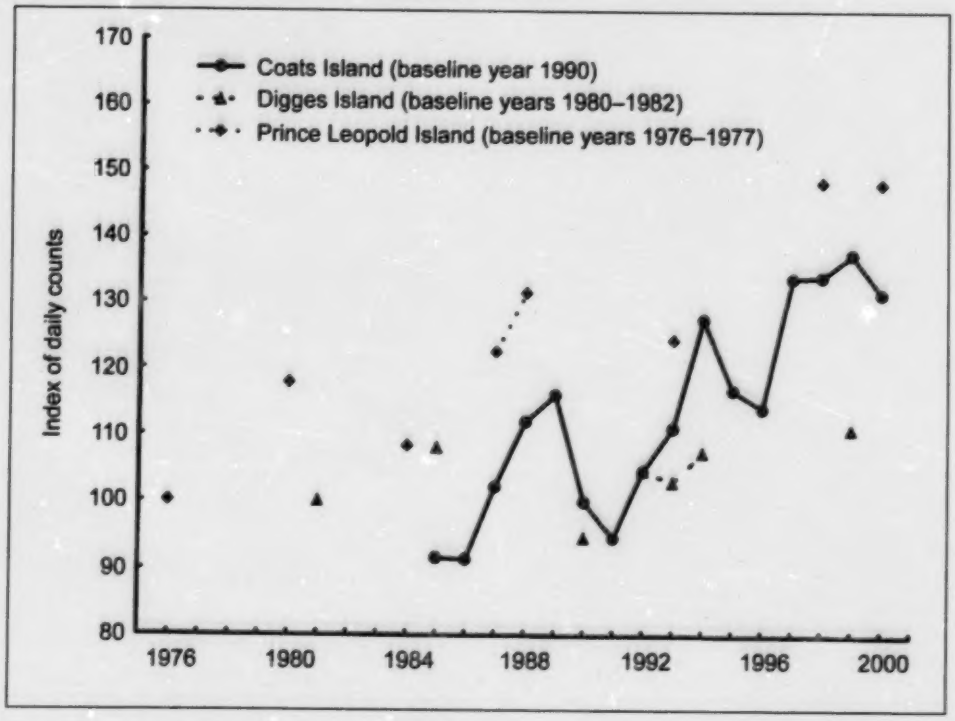


Figure 19
Trends in monitoring indices for all three colonies over the study period



some plots increased rapidly, while others remained more or less static or, in a few cases, exhibited nonsignificant decreases (Fig. 20). At Coats Island, changes at individual study plots from 1985 to 2000 varied from –16% (plots I and J) to +115% (plot D). Greatest increases were recorded for the peripheral study plots (Fig. 21), which averaged an increase of 80% (range +70 to +115%). Because the colony does not occupy the full height of the cliffs, new sites were added by upward colonization of unoccupied cliff areas (see Gaston et al. 1993).

At Prince Leopold Island, all but two of seven plots were bounded by the flat cliff top. Nevertheless, variation in rate of increase from 1976 to 2000 was similar to that seen at Coats Island, ranging from –1% at plot Q4 to +169% at plot G4. At Digges Island, only one plot was bounded by the cliff top, and changes in mean counts between 1980 and 1999 varied from –2% at plot B to +18.0% at plot H.

4. Discussion

4.1 Likelihood of observer bias or miscounting

A large number of observers contributed counts to the monitoring at all three colonies, although in some years most of the counts were made by one or two individuals. Despite this, all those in charge of counts in a given colony-year were trained by a single person (the author). Moreover, both the earliest and latest counts at Prince Leopold Island and those in most years at Coats Island were made by the author. Hence, the possibility that a "drift" in the counting methods has occurred appears unlikely. Provided that plot boundaries were correctly identified, reproducing counts was not difficult. Because birds, especially nonbreeders, came and went frequently, few counts were identical, but the criterion of repeatability within ±5 birds was not difficult to achieve, except in bad weather.

Comparability between years depended crucially on counts always being conducted from exactly the same spot. This applied particularly to plots where the cliff face was at a very oblique angle to the observer, because a small change in the position of the observer could either hide or reveal birds in crevices or behind jutting rocks. This problem was most acute at Coats Island, especially plots A and J. It hardly applied at Prince Leopold Island, where most plots were roughly at right angles to the line from the observer to the plot. This meant that, although plots were generally farther from the observer at Prince Leopold Island than at Coats Island, the Prince Leopold Island plots were generally easier to count. Digges Island plots were intermediate in ease of counting.

Misidentification of plot boundaries was a less likely source of error. However, the mean count at plot I, Coats Island, fell from 277 in 1985 to 204 in 1986, without any similar change at other plots. This was not remarked at the time, being early in the study, but such an abrupt change in a central plot was not observed subsequently and now appears very unlikely. It seems possible that either the count point or observers' understanding of the plot boundaries changed between 1985 and 1986.

4.2 Seasonal changes in attendance patterns

Seasonal patterns in attendance affect the choice of monitoring period in two ways: (a) a change in the mean numbers present during the course of the season means either that counts must be made at the same dates each year or that

Figure 20
Percent changes in mean counts during 1–7 August at Coats Island, Digges Island, and Prince Leopold Island

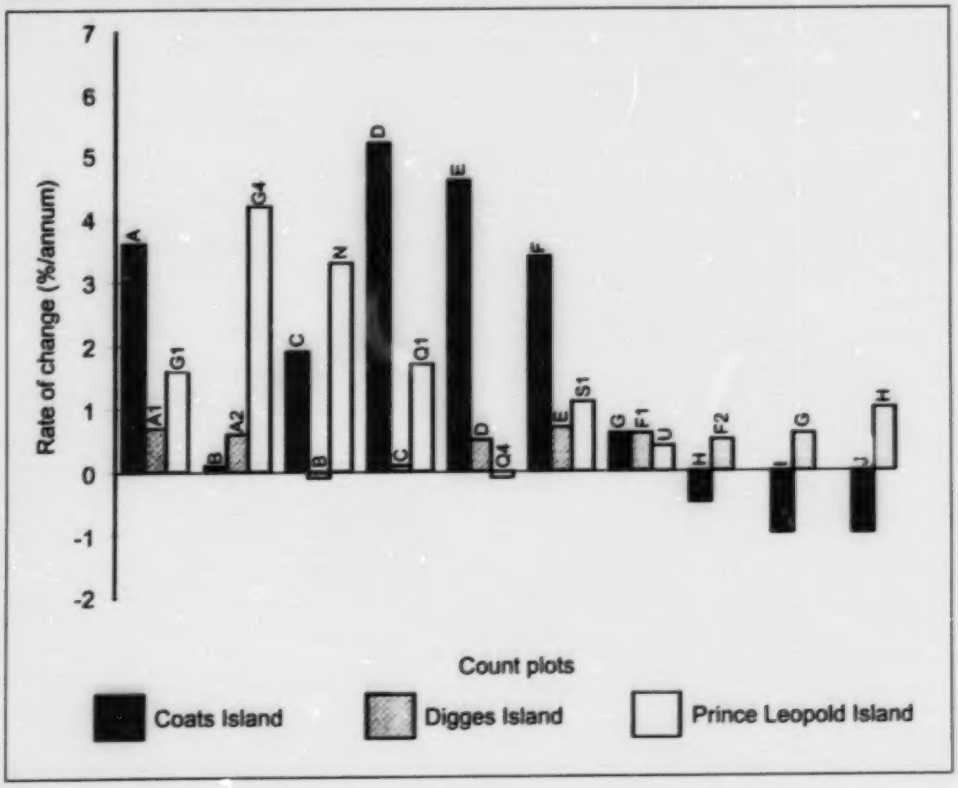
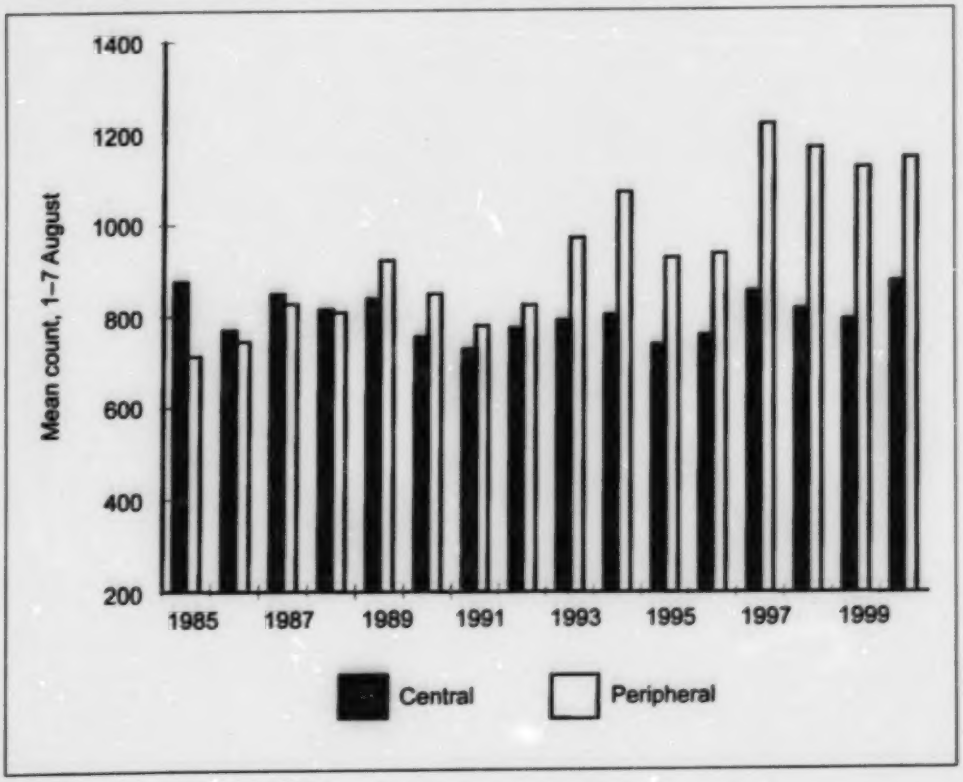


Figure 21
Mean number of murres counted on central and peripheral monitoring plots during 1–7 August in 1985–2000



some correction for date must be introduced; and (b) changes in the variability of counts will affect the precision with which means can be estimated and hence the confidence that can be placed in apparent trends.

Attendance patterns for *Uria* species have been described by Tuck (1961), Lloyd (1975), Birkhead (1978), Slater (1980), Gaston and Nettleship (1981), Birkhead and Nettleship (1987), Piatt and McLagan (1987), Rothery et al. (1988), and Hatch and Hatch (1989). In all studies, maximum numbers were usually counted during the period following median hatching, although Rothery et al. (1988) and Hatch and Hatch (1989) found substantial interyear variation. Seasonal trends differed mainly in the relationship of numbers during the laying and incubation periods to peak numbers. This relationship appears to be colony specific for Thick-billed Murres in the eastern Arctic, with both Digges and Prince Leopold islands exhibiting characteristic patterns. Although the seasonal trend in numbers at Coats Island was highly variable among years, the patterns never resembled those characteristic of the other two colonies.

Hatch and Hatch (1989) suggested that monitoring counts could be made with equal effectiveness from about median egg laying to the start of chick departures. For the three colonies considered here, peak numbers occurred on average between 3 and 15 August, despite the fact that laying at Digges and Prince Leopold islands averaged about 1 week later than at Coats Island. In addition to being the peak period for most colonies in most years, this period was also the period of lowest day-to-day variation at the three colonies. The fact that peak attendance and day-to-day variability appears to be related more closely to date than to the timing of breeding supports the conclusion reached by Gaston and Nettleship (1981) that attendance patterns are driven largely by the behaviour and attendance schedules of prospecting birds, rather than by the behaviour of breeding birds, determined by the breeding schedule. In any case, as observers will seldom be in a position to judge the timing of breeding before arrival at a given colony, a monitoring protocol based on date, rather than stage of breeding, is more practical. However, we need to bear in mind that alterations to breeding schedules as a result of climate change may render current recommendations obsolete eventually.

For the colonies considered here, the first half of August, corresponding roughly to the last 15 days before chicks begin to depart, appears to be the most suitable time for monitoring counts. As the colonies span the whole latitude range of Canadian Arctic colonies, this schedule is probably suitable for other colonies throughout the eastern Arctic. The intercolony and interyear variations in seasonal attendance patterns make the incubation period, especially the early part, less suitable. The relationship of counts at this stage of the breeding cycle to peak counts is more variable than during chick rearing.

4.3 Possible changes in the k-ratio

As indicated in the Introduction, all estimates of trends based on monitoring counts assume that the ratio of breeding pairs to total birds counted remains relatively constant from year to year. The close correlation between counts and numbers of breeding sites at Coats Island suggests that the k-ratio at that colony probably has remained fairly constant. However, the fact that the numbers of breeding sites rose faster than the counts after 1993, especially in 1998 and 1999, may indicate a progressive change in the k-ratio.

In 1999, the numbers of birds present on monitoring plots fell steeply after the middle of July. If the seasonal change in numbers had followed the usual trajectory, this decline would not have occurred, the counts in August would have been much higher, and the discrepancy between breeding sites and counts would have been much less marked. If the pattern of seasonal change in numbers recorded in 1999 becomes typical, this would affect mean k-ratios and would need to be considered in interpreting changes in monitoring counts. Further counts will be necessary to determine whether the environmental changes already detected at Coats Island (Gaston and Hipfner 1998, and unpubl. data) will alter the seasonal pattern of counts. If so, our protocols may need to be adjusted to take account of these changes.

4.4 Lessons for future monitoring

Despite the current monitoring scheme having been among the earliest to be established for *Uria* populations and designed at a stage when the species' biology was rather poorly known, the methods employed to date have yielded satisfactory results. The size of monitoring plots chosen corresponded to the later recommendations of Rothery et al. (1988), and the choice of time of day has proved appropriate. However, in retrospect, the choice of monitoring plots was not ideal, even given the constraint of choosing sites visible under most weather conditions. The following problems have been noted:

- At Coats Island, four out of 10 plots, including the two largest, were situated at the upper margin of the colony. Hence, as the colony has expanded mainly by spreading up the cliff, numbers on the monitoring plots probably have increased more than is typical of the whole colony.
- Defining plots by drawing boundaries tightly around occupied areas, especially at Prince Leopold Island, meant that subsequent expansion of some murre aggregations led to birds that clearly form part of the original grouping colonizing areas outside the original plot boundary.
- Plots close to one another tend to fluctuate in synchrony more than plots farther apart. Hence, the clumping of monitoring plots, especially plots D–F at Coats Island, is undesirable.
- Unevenness in the rate of increase of counts on different monitoring plots means that the combined total has come to be increasingly affected by a few large plots.

Selection of monitoring plots at other colonies should take these factors into account, where possible defining large plots containing roughly equal numbers of birds, containing substantial unoccupied areas, spread as far apart as possible, and facing the observer as squarely as possible. The more that the observer can view the plot from an angle perpendicular to the face of the cliff, the less likelihood there is that small changes in the position of the counting point will affect the results. In addition, a large number of plots should be selected and described (at least double the number to be counted) so that, if the number of birds counted on certain plots increases or decreases to the point where numbers fall

outside predetermined limits, additional plots can be added and the original plots discontinued after an overlap year in which both old and new plots are counted (as recommended by Harris et al. [1983]). The counts for the old plots in the overlap year can then be treated as a baseline for further counting. At Coats Island, it would probably be desirable to "cap" the size of the largest plot (A), which continues to expand rapidly up the cliff.

Although having the periphery of the colony over-represented in our study plots means that we may overestimate the rate of colony increase, it does allow us to detect increases that might go undetected if all the plots were defined in central parts of the colony. At Coats Island, central plots have shown no increase; the same applies to the small and very densely occupied plot Q4 at Prince Leopold Island. Provided that we understand the bias introduced by peripheral plots when a colony is expanding, their inclusion is probably desirable in any monitoring scheme, as they are likely to be more sensitive than central areas to changes in recruitment.

In addition to problems with the plots themselves, some monitoring counts were carried out during the early part of the incubation period, when day-to-day variation in counts was high, making them less reliable than counts carried out later in the season. Although confidence intervals on 7-day means remained fairly constant from 5 July to 20 August, interyear variation in the seasonal pattern of attendance meant that the average level of counts in July, relative to the year's peak, was less predictable than the levels during the first half of August. A combination of the low variation among counts (small confidence intervals relative to the mean) and their stability relative to peak numbers makes the first 10 days of August the best monitoring period for obtaining unbiased indices of population status.

4.5 Evidence for population change

The results of monitoring Thick-billed Murres in the eastern Arctic to date show that monitoring counts at all three colonies have increased, although the increase at Digges Island has been slight. In addition, the correspondence between the monitoring counts and the numbers of breeding sites on study plots at Coats Island, for the most part on different parts of the colony, suggests that the increase in the monitoring counts reflects an increase in the breeding population. It is worth noting that the observed overall rates of increase have been lower than the maximum rates observed for *Uria* populations elsewhere, where multiyear increases of up to 13% per annum have been reported (Stowe 1982, for Common Murres in the United Kingdom).

At present, little evidence is available to determine how the results of this monitoring match overall population trends. Gaston et al. (1993), using photo-counts, found that the population at the East colony on Coats Island had expanded by nearly 100% between 1972 and 1990 (mean annual increase 3.9%) and that of the West colony had increased at 1.6% per year between 1984 and 1990. The monitoring plots on the West colony suggest that the increase at the West colony has continued. There is also a small amount of evidence for colony expansion at Digges Island, where breeding birds have been found encroaching on grassy areas at the periphery of the colony throughout the monitoring period. However, these expansion areas appear to constitute only a small percentage of the total colony area.

Because monitoring counts for the peripheral plots at Coats Island have increased, while those for the central ones either have not increased or have shown only small increases, it appears that most central areas are saturated with breeding sites and that expansion can take place only by occupying areas outside the current colony boundary. Photographic evidence shows that the top boundary of the West colony has shifted upwards in many areas since 1972, especially at the south end of the colony (Gaston et al. 1993; AJG, unpubl. data). As the monitoring plots include a higher than average proportion of peripheral areas, the increase in the monitoring count is probably somewhat higher than the rate of increase in the total population over the same period. Considering the proportion of the colony represented by peripheral areas, the mean rate of increase for the colony between 1985 and 2000 was probably of the order of 0.5–1.0% per annum (hence the value assigned in Table 1).

4.6 Recommendations for future monitoring

Our monitoring plots constitute tiny samples of the colonies involved (at Prince Leopold Island and Digges Island, <0.5% of the total breeding population). These samples are much smaller than those used for Common Murres by the British monitoring schemes (lowest proportion among 20 plots reported by Rothery et al. [1988] in Britain was 3%), although the Canadian colonies are much larger. In addition, only three colonies are being covered, comprising about 20% of the eastern Arctic population of Thick-billed Murres. Moreover, the results of banding Thick-billed Murres at several colonies suggest that each colony has its own distinctive wintering behaviour, so the proportion of birds of different age classes that are shot in waters off Newfoundland varies greatly, and rather unpredictably, among colonies (Donaldson et al. 1997). In view of this, we might expect to find the effects of hunting varying widely among colonies. Although it is clearly impractical to monitor all colonies regularly, we should try to determine population trends for at least half of our colonies, especially the largest (Coburg Island, Cape Hay, The Minarets, and Akpatok Island North). Dragoo et al. (2000) outlined a similar strategy for Alaska.

The coincidence between fluctuations of monitoring counts at Coats and Prince Leopold islands suggests that population changes at these two colonies have been broadly similar over the past 15 years, despite the fact that the two colonies are at opposite ends of the species' breeding distribution in the eastern Arctic. Although the comparison is based on less frequent sampling, it appears that the Digges Island monitoring plots have undergone similar fluctuations. These indications suggest that, to monitor fine-scale changes in populations, it may be adequate to perform annual monitoring at one or two colonies only, confining monitoring at other colonies to longer intervals, with every 4–5 years being a reasonable schedule to aim at.

Because increases in population at all colonies appear to be achieved mainly through the colonization of additional areas for breeding, either on the periphery or on previously unoccupied areas within the main body of the colony, regular photographic records of the entire colony can provide a valuable indication of population change. Full photographic

records of each colony have been obtained regularly, and this practice should be continued (at least every 5 years) and the records compared with earlier series to identify boundary changes. Adequate storage and archiving of these photographic records should be an essential part of the monitoring program.

5. Afterword

The results presented here represent a very large investment in time and effort, as well as elements of hazard (off-strip landings, polar bears, cliffs, storms, etc.) that certainly exceed those encountered in typical work situations. Aircraft support, provided throughout by the Polar Continental Shelf Project of Natural Resources Canada, has amounted to the equivalent of more than a quarter of a million dollars for the Coats Island work alone. Although the Canadian Wildlife Service has an obligation to track population changes among harvested species, it might be difficult to justify the level of investment that has been expended over the years if this information had been the main rationale and major output of the work.

However, the original baseline studies all involved collecting a wide range of biological information on breeding and feeding ecology, contributing to a fundamental understanding of the species' biology. The subsequent monitoring of murres at Prince Leopold Island has been combined with monitoring of other seabird species, as well as sampling for toxic chemicals (Donaldson et al. 1998). At Coats Island, the counts have been made during banding operations to study survival and recruitment rates (Gaston et al. 1994; Gaston, this volume) and combined with observations of foraging and diet designed to track environmental changes in northern Hudson Bay (Gaston and Hipfner 1998). Similar banding and diet monitoring has been carried out during visits to Digges Island.

By combining population monitoring with collections for toxic chemical analysis, with sampling for diet, and with observations of breeding biology, we can place the results of population change in a broader context of environmental change. It is fortunate that the optimum period for making monitoring counts (early August) coincides with the best period for chick banding and for making observations of chick diets, the latter a sensitive indicator of changes in marine food webs in surrounding waters (Montevecchi 1993; Montevecchi and Myers 1995). We should ensure that the returns from the considerable sums expended to monitor seabirds in remote areas are maximized by increased collaboration, not only within the Canadian Wildlife Service, but with the Nunavut Wildlife Management Board, Parks Canada, the Department of Fisheries and Oceans, and other interested parties.

Acknowledgements

David Nettleship originally set the eastern Arctic monitoring scheme in motion and contributed to it substantially during the first decade. Richard Elliot and the Atlantic Region of the Canadian Wildlife Service contributed money and personnel to the Coats Island project in 1985–1987. Birgit Braune was extremely helpful in organizing and funding (through the Northern Contaminants Programme) the visits to Prince Leopold Island in 1993 and 1998. Additional funding and the loan of personnel for work at Coats Island in 1999 and 2000, and for the 1999 monitoring at Digges Island, were provided by Grant Gilchrist of the Prairie and Northern Region of the Canadian Wildlife Service.

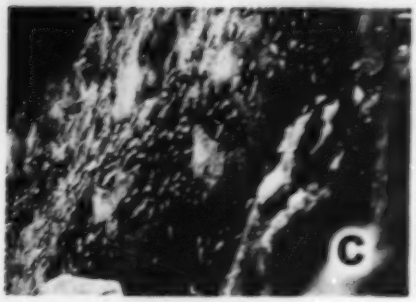
I am most grateful to all those who assisted with the monitoring counts over the years, especially, at Prince Leopold Island, Kate Beauchamp, Birgit Braune, Barbara Dodge, Garry Donaldson, Christine Eberl, Rod Forbes, Ilya Storm, and Stu Tingley; at Digges Island, Garry Donaldson, John Geale, Mark Hipfner, Vicky Johnson, Bruce Lyon, David Noble, Margie Purdy, Joe Spears, and Ilya Storm; and at Coats Island, Karel Allard, Anton Berto, Charlie Cornwallis, Leah de Forest, Sandra Dickman, Garry Donaldson, Richard Elliot, Grant Gilchrist, Graeme Gissing, Ellen Hayakawa, Mark Hipfner, Gabriella Ibarguchi, Christine James, Sue Johnston, Kaj Kampp, Clint Kelly, Kara Lefevre, Debbie Martin, David Noble, Sophia Perin, Paul Smith, Uli Steiner, and Kerry Woo. Thomas Alogut and Josiah Nakoolak kept us safe from bears. None of this work would have been possible without the logistical support of the Polar Continental Shelf Project of Natural Resources Canada and the Nunavut Research Station (formerly the Iqaluit Laboratory of the Department of Indian Affairs and Northern Development), as well as the financial support of the Canadian Wildlife Service and the Offshore Labrador Project of Petro-Canada.

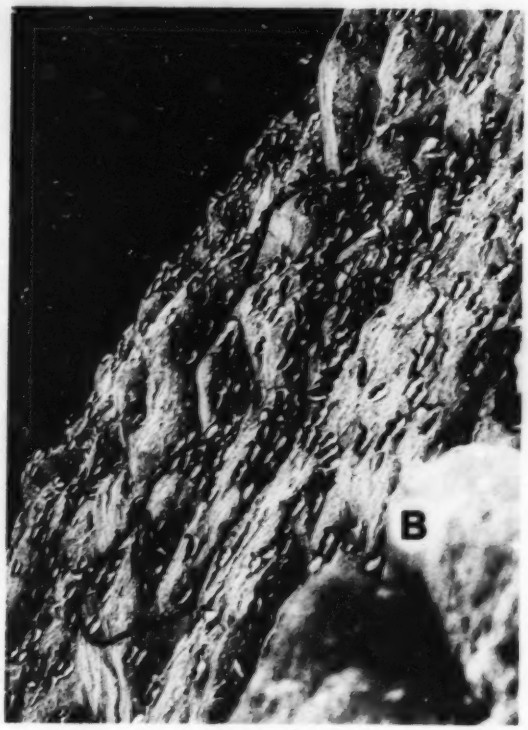
The manuscript benefited from comments by Peter Blancher, Hugh Boyd, Kees Camphuysen, John Chardine, Brian Collins, and Scott Hatch. I am most grateful to Bill Montevecchi for writing the foreword to this volume.

Appendices

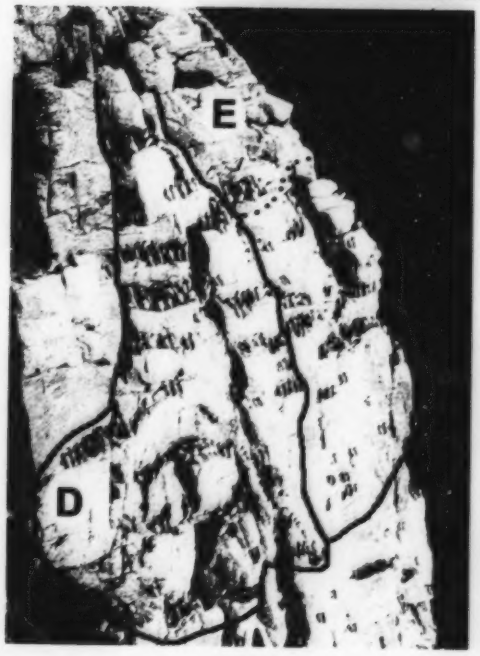
Appendix 1
Photographs of study plots at Coats, Prince Leopold, and Digges islands counted as part of the ongoing population monitoring program and used in the analyses presented

Coats Island





DA
D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F

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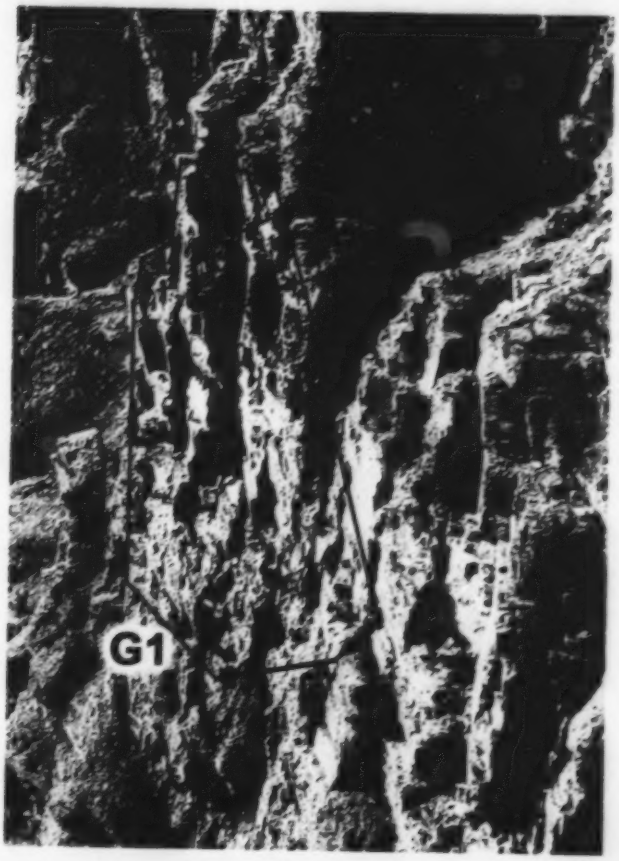
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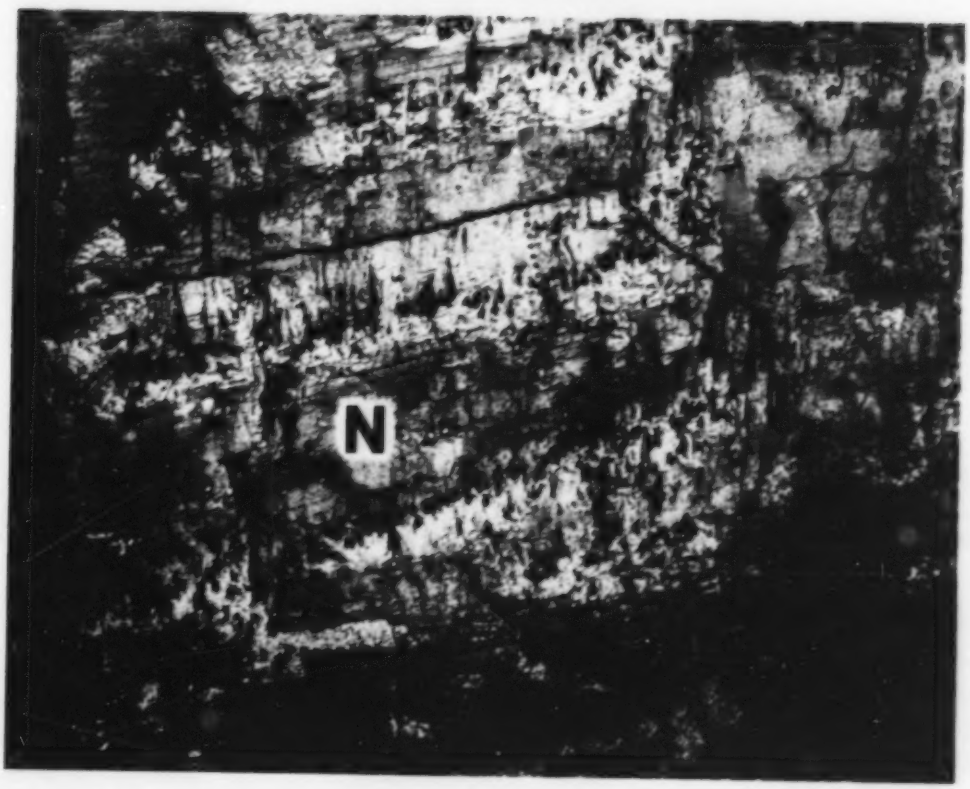
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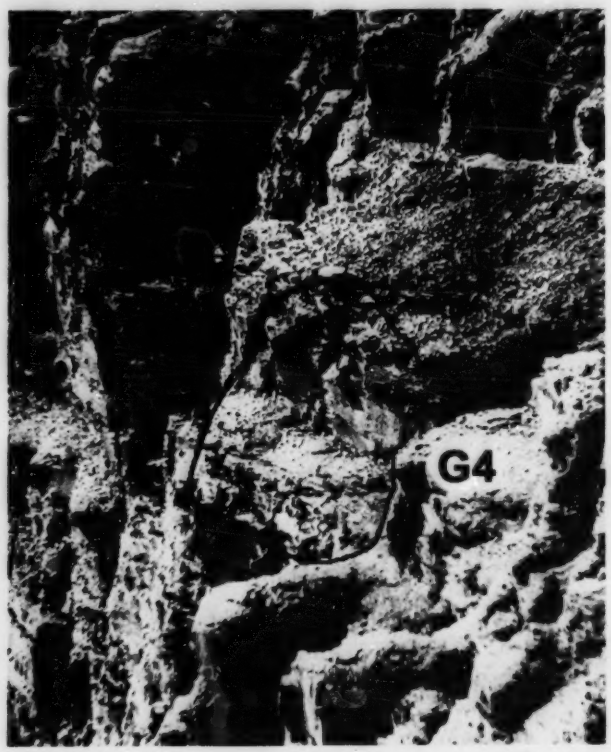
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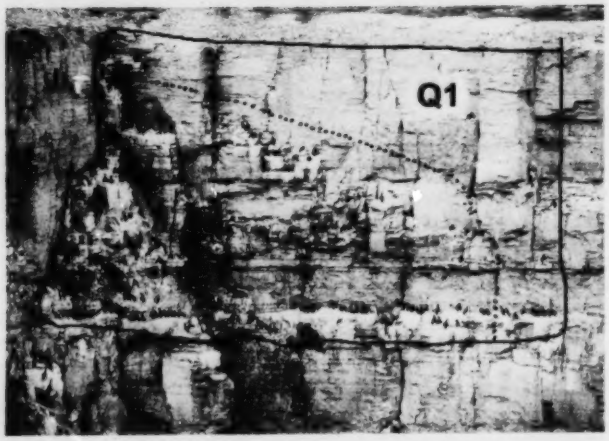
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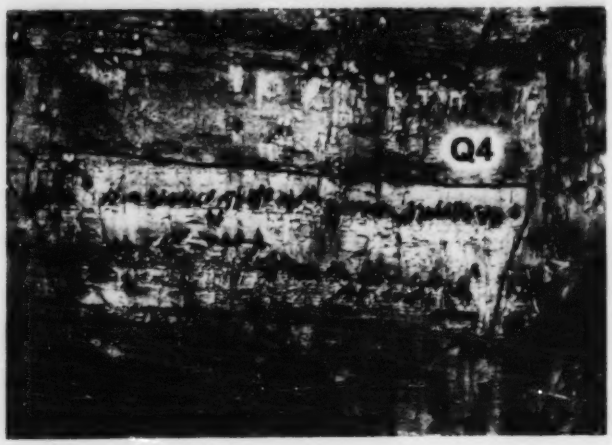
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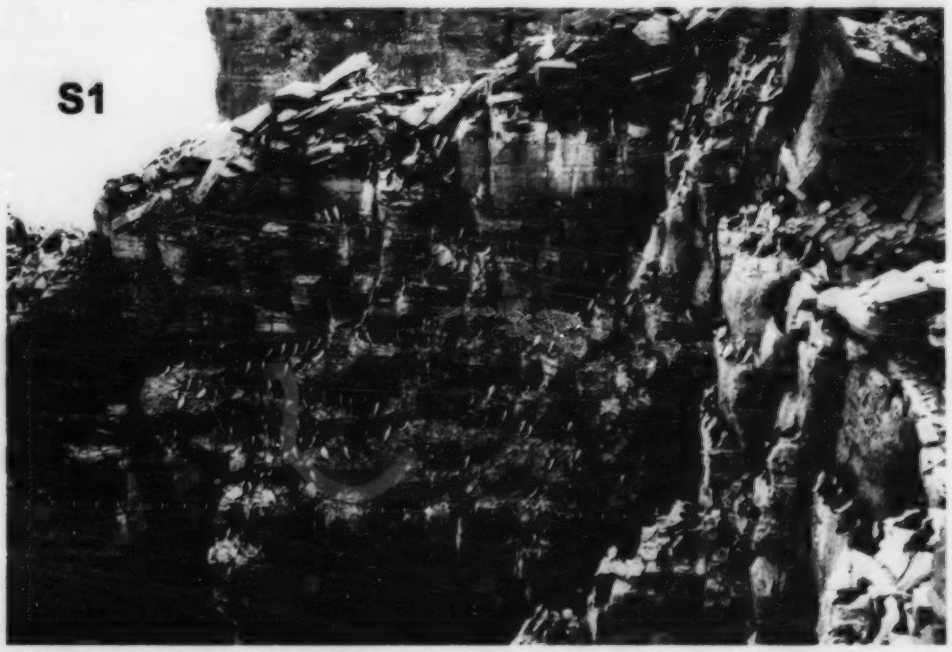
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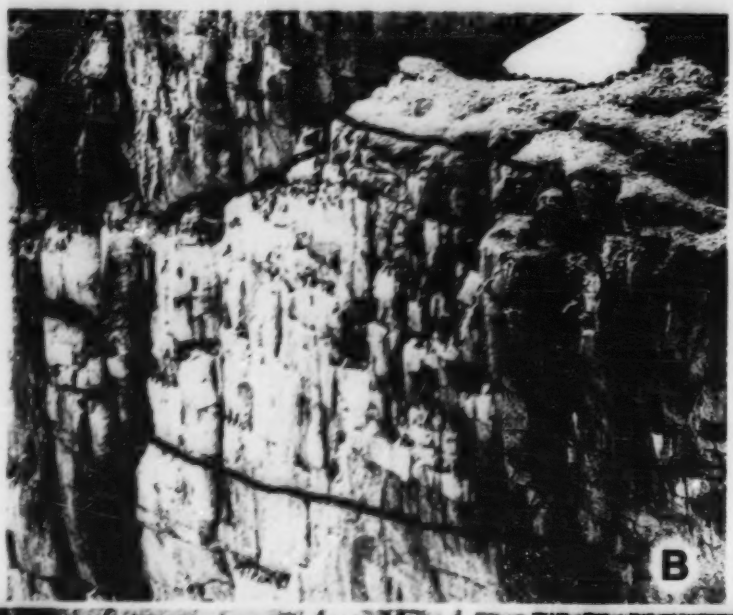
U

A1
A2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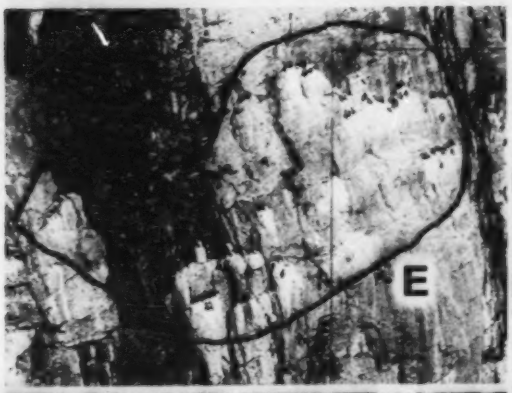
E

F2

F1

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H

Appendix 2
Daily counts at Coats Island (sum of A–J)

Date	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000
1 June																
2 June																
3 June						1778										
4 June																
5 June																
6 June																
7 June																
8 June						1868					0					
9 June											372					
10 June											921					
11 June						996				1647	1108					
12 June						1361				871	858					
13 June				869						687	733	1128				
14 June				1295			1070	1870		846	1179	1310				
15 June				760			1114	126		1812	1083	1283	1742			
16 June				284		1732	822	3		1081	1480	1106	1747			
17 June				1611		1373	1110	1620		1604	1451	606	1630			
18 June				1252		543	1398	594		1283	1678	1382	1709			
19 June				1251		1112	1130	695		1372	1553	880	1634			
20 June				1362		1325	1015	1204		1558	1798		1753	1504		
21 June				1408		1010	816	978		1572	1455	935	1466	1611		
22 June				1419		1265	1300	752		1572		1481	1992	1598		
23 June				1358		825	765	1111		1162	1264	1699		1754		
24 June				1057		1090	1411	1232		1984	1775		1834	1635	1469	
25 June				1517		1355	1274	647		1833		1364	1714	1433	2238	
26 June				1720		939	1084	1611		1844	1684	1437	1868	1904	1945	
27 June				1454		1514	1346	1432		1498	1939	1489	1912	1830	1999	
28 June				1622		1467	1214	1006		1930	1741	1484	1771	1775	1539	
29 June				1662		1223	1222	1435		1735	1810	1378	1724	1796	2081	
30 June				1470		1221	1460	1493		1819	1433	1535	1674	1814	2176	
1 July				1723		1559	1198	1694		1640	1509			1808	2086	
2 July				1617		873	1518	1412		1801	1613	1536	1682	1769	2109	
3 July				1565		1226	1354	1687		1688	1740	1635	1816	2040	2075	
4 July				1555		1579	1459	1584				1505	1757	1946	2105	
5 July				1510		1258	1387	1641		1879	1475	1608	1797	1630		
6 July				1686		1450	1190	1369		1685	1470	1560	1952	1977	2039	
7 July				1672		1592	1265	1815		1755	1301	1553	1840	1599	2146	
8 July				1734		1348	1455	1586		1688	1256	1576	1912	1835	2109	
9 July				1742		1533	1456	1459		1624	1653	1358	1835	1722	2046	
10 July				1583		1592	1101	1313		1683	1442		1855	2043	1919	
11 July				1648		1383	1222	1265		1655	1316		1827		2262	
12 July				1496		1348	1278	1557		2030	1679	1626	1947	1715	1998	
13 July				1528		1489	1352	1629		1845	1902	1530	1637	1884	2069	
14 July				1515		1383	1452	1492		1817	1696	1226	1700	1887	2021	
15 July				1594		1409	1016	1577		1616	1497		1733	2008	2103	
16 July				1568		1527	1504	1680		1761	1686	1530	1985	1905	2366	
17 July				1551		1397	1368	1602	1578	1808	1632	1514	2046	1759	1976	
18 July				1504		1413	1374	1612	1597	2012	1799	1651	2074	1878	2245	
19 July				1432		1428	1360	1342	1605	1962	1663		1854	1925	2153	
20 July				1603		1383	1014	1477	1530	1778	1947	1665	2105	1942	2109	
21 July				1507		1479	1576	1774	1592	2000	1780	1675	1942	1962	2092	
22 July				1534		1540	1186	1469	1654	1859	1726	1673	1897		1793	
23 July				1633		1231	1439	1588	1712	1839	1830	1685	1944	1859	1793	
24 July		1264		1468		1352	1524	1541	1674	1753	1510	1620	1555	2112	1955	
25 July		1271		1847		1630	1330	1562	1607	1771	1261		2010	2025	1881	
26 July		1373	1515	1728		600	1137	1540	1663	1722	1702	1748		1605		
27 July		1491	1278	1283		1717	1495	1554	1731	1833	1630	1738	1986	1928	2015	
28 July		1506	1438	1782		1000	1483	1547	1780	1317	1412	1790	2101		1884	2046
29 July		1289	1571	1641	1942	1187	1435	1571	1605	1966	1682	1817	2157	2054	1880	1895
30 July		1536	1638	1762	1780	1540	1371	1626	1683	1880	1776	1812	2103	2021	1964	1547
31 July	836	1613	1650	1601	1842	1572	1460	1553	1735	1883	1646	1758	2073	2021	1851	2337

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Appendix 2 (*cont'd*)
Daily counts at Coats Island (sum of A–J)

Date	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000
1 August	1284	1267	1713	1645	1849	1605	1549	1668	1880	1984	1485	1620	1994	2044	1928	2244
2 August	1450	1295	1648	1734	1830	1511	1529	1615	1826	1796	1634	1544	2156	2090	2094	2025
3 August	1507	1499	1743	1689	1799	1697	1501	1646	1691	1956	1757	1628	2086	1945	1945	1989
4 August	1693	1573	1743	1702	1811	1597	1457	1565	1849	1936	1562	1734	2052	1958	1874	1958
5 August	1650	1518	1650	1304	1812	1557	1545	1468	1698	1797	1655	1773	1974	1867	1918	2137
6 August	1765	1445	1584	1474	1788	1597	1453	1686	1701	1818	1790	1658	2146	2029	1829	2212
7 August	1067	1255	1659	1832	1767	1574	1526	1561	1709	1857	1796	2011	2153		1875	2131
8 August	1797		1588	1746	1806	1759	1492	1511	1749	1896	1585		2089	2118	1714	2197
9 August	1739		1453	1676	1716	1777	1458	1461	1688	1553	1838	1792	1809	1922	1592	2143
10 August	1573		1608	1664	1830	1577	1617	1527	1588	1913	1786		1856		1835	2063
11 August			1603	1839	1733	1594	1334	1502	1661	1718	1788	1807	2131			1700
12 August				1724	1741	1597	1616	1452	1720	1718	1452	1840	1970		1637	2092
13 August			1751	1717	1698	1651	1589	1549	1224	1861	1721	1714	1955		1828	
14 August			1772	1734	1622	763	1623	1552	1790		1559	1641	1863		1486	
15 August			1702	1625	1721	1312	1484	1525	1701	1694	1799	1841				1849
16 August			1566	1623	1543	1563	1372	1438	1740	1524	1832	1709				1859
17 August			1540		1673	1553	1343	1495	1599	1576	1442					
18 August						1485	1355	1536	1499	1668	1357	1575				1649
19 August						1470	1512	1202	1496		1327	1582				1630
20 August						1492	1669	1529	1414	1569	1300	1618				
21 August						1500	1332	1448		1713	1398					
22 August						1257	1209	1240		1665	1237					
23 August						1211	1128	1439			1345					
24 August							1166	1238								
25 August							972				341					
26 August							1031				756					
27 August							258				821					
28 August																
29 August											546					
30 August											408					
31 August											208					
1 September											140					
2 September											73					
3 September											13					
4 September											14					
5 September																
6 September																
7 September																

Appendix 3
Daily counts at Prince Leopold Island (sum of G1, G4, N, Q1, Q4, S1, and U)

Date	1976	1977	1976–1977 mean	1980	1984	1987	1988	1993	1998	2000
20 June	593		593							
21 June	596		596							
22 June	743	939	841							
23 June	680	624	652							
24 June	678	624	651							
25 June	489	620	554.5					975		
26 June	726	618	672					671		
27 June	670		670							
28 June	836	654	745					844	1298	
29 June	767		767					1257	990	
30 June	702		702					391	1283	
1 July	874	919	896.5					1097	1230	
2 July								784	1259	
3 July	870		870					1437	1144	
4 July	903	882	892.5					1272	1221	
5 July	706	963	834.5					678		
6 July	825	825	825							
7 July	805	851	828							
8 July	720	849	784.5							
9 July	765	846	805.5							
10 July	759	803	781							
11 July	813	894	853.5							
12 July	668	945	806.5							
13 July	760	823	791.5							
14 July	785	784	784.5							
15 July	784		784							
16 July	799		799							
17 July	820		820							
18 July	796	1000	898		984		1246			
19 July	823	928	875.5		987		1184			
20 July	900	959	929.5		1105		871			1271
21 July	802	874	838		1009		1317			1269
22 July	781	892	836.5		943		1239			1321
23 July	751	931	841		926		1248			
24 July	859	988	923.5	967	922		1212			1372
25 July	817	994	905.5	1192	972		1166			
26 July	860	1039	949.5	1078	898					
27 July	848		848	982	917					
28 July	791	1003	897	1108	1111		1245			1417
29 July	918	1001	959.5		906		1288			1365
30 July	857	1093	975	1143	1067	1217	1148			1404
31 July	810	1097	953.5	1169	942	1158	1252			1369
1 August	997	1088	1042.5	1171	1076	1168	1281			1407
2 August	872		872	1097		1157				
3 August	875		875	964		1063				1462
4 August	931	1033	982				1271			1429
5 August		1093	1093							
6 August	921	1039	980			1202	1215			
7 August	695	968	831.5				1176			1459
8 August	974	1057	1015.5				1160			
9 August	934	1014	974							
10 August		1008	1008							1249
11 August		1018	1018							1448
12 August	896	1003	949.5							1397
13 August	976	1074	1025							1403
14 August	844	958	901							
15 August		869	869							1361
16 August	959	998	978.5							1406
17 August	839	911	875							1338
18 August	845		845							

Continued on next page

Appendix 3 (*cont'd*)
Daily counts at Prince Leopold Island (sum of G1, G4, N, Q1, Q4, S1, and U)

Date	1976	1977	1976–1977 mean	1980	1984	1987	1988	1993	1998	2000
19 August	810		810							
20 August	788	956	872							
21 August	798	873	835.5							
22 August	328	806	567							
23 August	451	836	643.5							
24 August	386	789	587.5							
25 August		842	842							
26 August	237	718	477.5							
27 August	178	605	391.5							
28 August	88	650	369							
29 August	94	478	286							
30 August	68	326	197							

Appendix 4
Daily counts at Digges Island (sum of A1, A2, B–E, F1, F2, G, and H)

Date	1980	1981	1982	Mean of 1980–1982	1985	1990	1992	1993	1994	1999
14 June			1737	1737						
15 June			914	914						
16 June			9	9						
17 June			301	301						
18 June			886	886						
19 June			1691	1691						
20 June		417	1121	769						
21 June		1192	505	849						
22 June		1546	1304	1425						
23 June		1204	1574	1389						
24 June		869	1082	976						
25 June			931	931						
26 June		1236	1190	1213						
27 June		1455	1310	1383						
28 June	1215		1144	1180						
29 June	1235	1278	1267	1260						
30 June	1168	1583	1671	1474						
1 July	1361	1315	1123	1266						
2 July	1194	889	1321	1135						
3 July	1420	906	1458	1261						
4 July	1665	1610	1443	1573						
5 July	1344	1288	1272	1301						
6 July	1315	1456	1331	1367		1217				
7 July	1115	1274	1222	1204		1142				
8 July	1334	1223	1368	1308		1186				
9 July	1709	1301	1720	1577		1190				
10 July	1319	1278	1598	1398		1603				
11 July	1598	1429	1358	1462		1637				
12 July	1576	1435	1546	1519		1098				
13 July	1395	1393	1685	1491		1147				
14 July	1453	1584	1607	1548		1537				
15 July	1131	1253	1538	1307		1593				
16 July	1624	1523	1583	1577						
17 July	1773	1332	1502	1536						
18 July	1460	1562	1750	1591						
19 July	1578	1674	1774	1675						
20 July			1223	1223						
21 July	1725		1527	1626	1854					
22 July	1731	1316	1662	1570	1512					
23 July	1385	1537	1796	1573	1679				1763	
24 July	1726	1810	1728	1755	1764				1320	
25 July	1033	1295	1655	1328	1731				1516	1752
26 July	1941	1652	1670	1754	1748				1785	1471
27 July	1690	1689	1736	1705						1882
28 July	1159	1211	1726	1365					1776	1727
29 July	1718	1199	1487	1468				1649	1629	1507
30 July	1495	1878	1201	1525				1606	1603	
31 July	1515	1572	1900	1662				1680		1892
1 August	1425	1663	1579	1556					1683	1714
2 August	1634	1573	1590	1599				1746	1736	1755
3 August	1357		1737	1547				1723		1825
4 August	1706	1515	1711	1644				1615	1780	1810
5 August	1667	1586	1710	1654				1596		1681
6 August	1293	1592	1628	1504				1554		1698
7 August	1565	1616	1513	1565				1647		
8 August	1529	1553	1636	1573				1453		
9 August		1594	1691	1643						
10 August	1508	1617	1581	1569				1647		

Continued on next page

Appendix 4 (*cont'd*)
Daily counts at Digges Island (sum of A1, A2, B–E, F1, F2, G, and H)

Date	1980	1981	1982	Mean of 1980–1982	1985	1990	1992	1993	1994	1999
11 August	1641		1499	1570			1676	1410		
12 August	1611		1625	1618			1585	1417		
13 August	1577	1616	1556	1583			1719			
14 August	1658	1530	1390	1526			1520	1903		
15 August	1591	1620	1666	1626			1581			
16 August	1643	1401	1392	1479			1704			
17 August	1483	1582	1507	1524			1483			
18 August	1551	1164	1570	1428			1728			
19 August	1416	1683	1654	1584			1563			
20 August	1388	1582	1546	1505			1535			
21 August	1508	880	1465	1284			1070			
22 August	1467		1410	1439						
23 August	1300		1434	1367						
24 August	1617	937	1214	1256						
25 August	1404	1634	1399	1479						
26 August	735	1047	766	849						
27 August	918	962	1388	1089						
28 August	1424	1266	1254	1315						
29 August	1091	485	833	803						
30 August	474	1292	1035	934						

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